THE OBJECT-ORIENTED SIMULATION ON THE COMMUNITY STRUCTURE OF A CORAL COMMUNITY IN PING CHAU, HONG KONG

by

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ABSTRACT

Scleractinian coral community is one of the complex communities that exhibit extreme variation in community structure and diversity (Connell, 1973; Sorokin, 1993). However, mechanisms governing the stability of this community are still not completely known. In Hong Kong, the degradation of marine and coastal environment was observed everywhere. Therefore, developing an ecological model to understand mechanisms governing the dynamical behaviour of a coral community may become urgently needed to help protect and conserve these delicate marine communities.

Field studies on a selected coral community in A Ma Wan of Ping Chau, on the north-eastern part of Hong Kong was conducted. A preliminary survey by continuous transect recording and quadrat-area method was initially carried out in 1996 to identify the dominant groups of corals found in the study area. Five dominant groups of corals were recognized and they were massive-form or castle-like corals of Family Faviidae, foliaceous *Pavona decussata* of Family Agariciidae, branching or tabular form corals of Family Acroporidae, mushroom-like corals with elongated polyps (belonging to genera *Goniopora* or *Alveopora* of Family Poritidae) and massive-form *Porites lobata* of Family Poritidae.

An extensive field survey on the coral community in the study area was subsequently conducted in early 1997 after the preliminary study. An approximate area of 3,600 m^2 was covered. Species diversity and coral cover on 79 0.5m x 0.5m quadrats based on systematic quadrat-area method were evaluated. Twenty-five hermatypic scleractinian

coral species, belonging to nine families, were identified in this study. Total coral cover was found to be 51.82% and the overall Brillouin Index of species diversity calculated was 1.021. *Goniopora columna*, *Montipora informis*, *Pavona decussata*, *Platygyra sinensis* and *Porites lobata* were the five dominant species found. Among the corals identified, *Platygyra sinensis* was the most dominant species with about 26% relative abundance. Zonation pattern was observed in the coral community studied. This pattern might be due to exposure to different types and degrees of disturbance that occurred in different parts of the study area. Such large area of coral community in Ping Chau with high species richness should receive serious concern for its conservation.

An object-oriented computer model was developed to simulate the dynamical behaviour of a coral community with five dominant groups of corals identified in the preliminary study. Effects of different levels of disturbance on the dynamical structure of the simulated coral community were investigated. Fast-growing habit with overtopping competitive mechanism was found to be one of the powerful strategies for a coral to gain dominance in a stable environment. High species diversity in a coral community was maintained by intermediate level of disturbance. In addition, different coral groups become dominant under different levels of disturbance. Disturbance and biological responses to disturbance may be the main structuring factors of the coral community in an unstable reef environment.

Coral community structure observed from the extensive field study in two out of the six zones of the study area were found to be similar to that generated from the computer simulation. Much improvement in the ability of the computer model to simulate the dynamics of the coral community is expected when information on the behaviours of the dominant coral groups towards disturbance, the *in-situ* records of physical conditions and disturbance, and interacting effects from other groups of organisms observed in the study area could be incorporated into the model.

香港平洲的珊瑚群落結構之物件導向電腦模擬

譚子慧
香港中文大學
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摘要

造礁石珊瑚群落是一種複雜的群落，它擁有極其多變的群落結構及品種多樣性 (Connell, 1973; Sorokin, 1993)。 然而，控制此群落穩定性的機制仍未完全清楚。在香港，各處的海洋及沿岸生態環境逐漸惡化，爲了保育這些易受破壞的海洋生物群落，建立一個生態模擬系統去研究控制其動力行爲之機制，是必須及急切的。

平洲位於香港的最東北方, 而位於此小島之阿媽灣珊瑚群落被選作研究之用。一個初步的調查於1996年開始進行。 此調查是用連續紀錄及方框面積兩種方法，去確認在研究區內最重要的珊瑚組別。有五組珊瑚被確認，它們分別爲蜂巢珊瑚科 (FamilyFaviidae) 裡大塊狀或堡壘狀的珊瑚、菌珊瑚科 (Family Agariciidae) 裡薄葉狀的十字牡丹珊瑚 (*Pavona decussata*)、鹿角珊瑚科 (Family Acroporidae) 裡枝狀或圓桌狀的珊瑚、屬於濱珊瑚科 (Family Poritidae) 裡角孔珊瑚屬 (Genera *Goniopora*) 或 *Alveopora* 屬的延長蝕狀體菇狀珊瑚、及濱珊瑚科 (Family Poritidae) 裡大塊狀的濱珊瑚 (*Porites lobata*)。

繼初步調查後，一個比較深入及密集的調查於1997年初期逐步進行。 調查面積大約有3,600平方米，用了79個面積同是 0.5m x 0.5m 的方框 (根據系統性的方框面積方法) 來評估方框內珊瑚所佔的面積及其多樣性。有二十五種屬於九個科的造礁

石珊瑚品種被確認。 計算結果發現珊瑚的總面積是51.82%，而品種多樣性指數 (Brillouin Index of diversity) 爲1.021。另外，五種覆蓋面最廣的珊瑚品種包括角孔珊瑚 (*Goniopora columna*), 薔薇珊瑚 (*Montipora informis*), 十字牡丹珊瑚 (*Pavona decussata*), 中華扁腦珊瑚 (*Platygyra sinensis*) 及濱珊瑚 (*Porites lobata*)。在此五種珊瑚中，中華扁腦珊瑚是最重要的，其所佔的面積有26%。此外，可能不同部份的研究地區受到不同程度及不同種類的擾亂，所以在那裡的珊瑚群落出現了分層的現象。 因爲平洲的珊瑚品種數量很高及擁有覆蓋面很廣的珊瑚群落，所以那處的海洋環境是應受到重視及保育的。

一個物件導向的珊瑚群落之電腦模擬系統在此研究項目下建立。 此電腦系統是用以模擬在初步調查裡所找到五組最重要的珊瑚組別之動力行爲，同時亦調查不同程度的擾亂對摸擬之珊瑚群落的動力結構影響。結果顯示在穩定的環境中，生長速度比較快及擁有遮蓋形式競爭力的珊瑚比較容易擴大自己的群落，而中等程度的擾亂可維持珊瑚群落較高的品種多樣性。在不穩定的珊瑚礁環境，擾亂及面對擾亂的生物反應，可能是影響珊瑚群落結構的最主要因數。

在平洲的野外研究地區被劃分成六個區域，從深入及密集的研究結果顯示，兩個區域的珊瑚結構被發現與電腦模擬的結果相似。強盛的珊瑚組別面對擾亂行爲的資料，原處的物理條件及擾亂程度，以及在研究地區內其他物種和珊瑚的相互反應，都應加入模擬系統內，以改善此模擬系統的眞確性。

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CHAPTER 1 INTRODUCTION

1.1 Modelling the Dynamics of a Coral Community

Coral reef communities are one of the most diverse marine communities in which everything is tightly recycled and inter-dependent. Coral reef communities are fascinating and have high ecological and economic values (Scott, 1984; Sale, 1988; Weber, 1993). Scleractinian coral community of the coral reef ecosystem is one of the complex communities that exhibit extreme variation in community structure and diversity (Connell, 1973; Sorokin, 1993). Each coral species in this community has been demonstrated to possess a wide range of biological characteristics and various sensitivities to different environmental conditions (e.g. Kinsman, 1964; Baker and Weber, 1975; Riegl, 1995). Diverse types of interspecific and intraspecific interaction have also been identified in this community (Land and Chornesky, 1990).

However, coral reef communities are very sensitive to both natural and anthropogenic disturbance. Significant changes in the diversity and structure of coral communities have been shown after physical disturbance (e.g. hurricane) (Woodley *et al.*, 1981; Dollar and Tribble, 1993; Andres and Witman, 1995). Immediate structural changes have occurred in reef benthic (e.g. Porter *et al.*, 1981; Rogers *et al.*, 1991; Bythell *et al.*, 1993) and fish communities (Chabanet *et al.*, 1995) after the impact of hurricanes. Damage to coral reefs has also been documented by the effect of El Niño event (Brown and Suharsono, 1990) and by human impacts (Sakai and Nishihira, 1991; Hunter and Evans, 1995). Aronson and Precht (1995) provided the first quantitative evidence for intermediate disturbance effects in coral assemblage.

Nowadays, coral reefs are among the most endangered ecosystems on earth (Weber, 1993). A survey in the 1980s found that damage to coral reef had occurred in 93 of the 109 countries with reefs and coral communities (Wells and Hanna, 1992). The mechanisms governing the stability of coral reef communities are still not completely known. Developing an ecological model to understand the behaviour of a complex system is one of the useful ways to study the critical point of stability and the dynamics of these sophisticated systems. The reliability of ecological model should be verified since they are only "abstraction" of the natural systems. As the essence of developing ecological model is to understand the actual behaviour of natural system, evaluation of field data inevitably becomes one of the necessary approaches and the most powerful way for testification of the developed models. Modelling of a scleractinian coral community can provide an insight on the dynamical behaviour of such a complex system towards different degrees of disturbance. Together with verification of field results, models should provide a powerful tool for the investigation of the behaviour of this complex ecological system. The mechanisms governing the stability of a coral reef ecosystem could thus be better understood.

1.2 New Paradigm in Understanding Complex System

Traditionally, simple deterministic models were developed to study simple systems and the world defined by science was an almost Platonic purity. Regularity, clockwork-like certainty and linearity have been thought of as the laws of nature which allow people to explain and predict the behaviour of inside systems. However, turbulence, irregularity and unpredictability are everywhere. Such unusual dynamical behaviours were not given serious relevance until the past twenty years. A fresh concept of wholeness, complexity and chaos is now at the heart of a revolution to understand nature.

Simple deterministic ecological models have been found to exhibit very complicated behaviour by May (1974, 1976), and have raised much interest among population biologists to re-investigate the models. A three-species model has already been demonstrated to exhibit very complex dynamics (Hastings and Powell, 1991). Typically, equilibrium points (constant population densities), limit cycles (periodic oscillations) and chaos (irregularly fluctuations governed by strange attractors) were observed in low-dimensional systems.

The inherent feedback feature of nonlinear models inevitably governs complex dynamics of a sophisticated system. Both negative feedback and positive feedback properties can exist to determine the behaviour of a complex system. A system can be stabilized by staggering number of negative feedback loops built up inside, or it can be completely disorganized with amplifying effects of the positive feedback interactions between individuals. Feedback embodies an essential tension between order and chaos in a complex system (Briggs and Peat, 1989).

Identification of feedback nature of a complex interconnected system implies that a system cannot be isolated into different small parts for investigation. Such isolation will completely ignore the effects of feedback interaction between different parts of the system. Overall system behaviour thus cannot be understood from the study of its isolated parts. *Behaviour of the whole is different from the sum of its parts* (Langton,1989a).

A different paradigm should be constructed to understand nature. As chaotic characteristics of a nonlinear system make its dynamics very sensitive to initial condition, any precise prediction of the system's long-term behaviour becomes unrealistic. Sharping the model to make a forecast about future events should no longer be a focus in ecological modelling. In addition, as the "whole" should be considered instead of the parts of system, understanding the critical points and mechanisms governing the stability of a system will be one of the new guidances.

1.3 Ecological Models under the New Paradigm

Many classical ecological models are simple abstraction of the real dynamical behaviour of natural system which typically focus on two-species interaction. However, organisms in nature are embedded in a complex interconnected communities. Applying two-species model in ecological studies hence can only account for a small number of the phenomena commonly exhibited in nature. Dynamical behaviour of each organism in the system can be revealed only by modelling the interactions of three or more species.

Many new ideas have recently been introduced to study the complex biotic or ecological systems. A computer system, called random Boolean NK networks, has been introduced by Kauffman (1991) to model complex biological phenomena. The Boolean network is governed by a logical switching rule called Boolean function. The network is composed of *N* elements linked by *K* inputs per element. Inputs and one of the possible Boolean functions are assigned at random to each element. By assigning values to N and K, one can define an ensemble of networks with the same local features. This network model has been successfully used to simulate the responses of a complex community structure to species interactions driven by phenotypic change (Dodds and Henebry, 1995).

The concept of "autopoiesis", which gives the living systems unique characteristics by possessing property of constant self-renewal through a staggering number of feedback loops built up in the systems, has also been proposed as the mechanism for stabilization in a sophisticated, interconnected structure (Briggs and Peat, 1989). Such idea of "self-organization" provides a basic philosophical background to understand a complex system.

However, the assumption of most models still violates two basic tenets of biology (Huston *et al.*, 1988). First, these models often combine many individual organisms and assume that they can be described by a single variable, e.g. population size. Such characterization of large numbers of organisms by some overall or average property violates the principle of "individuality" - the phenotype and behaviour of each organism are different and are unique in nature.

Second, most simulations do not distinguish among organisms' locations. They have no real spatial representation and do not model spatial variability. Each individual in the simulations is assumed to have an equal effect on every other individual. Local interaction is thus omitted. However, an organism is affected primarily by other organisms with which it comes into contact. Therefore, such assumption of equal effect violates the biological principle that interactions are inherently local.

In order to address the violation of the two basic biological tenets mentioned in most ecological models, idea of individual-based approach has been developed in the last ten years to model the ecosystems. (e.g. Huston *et al.*, 1988; Stone, 1990; Sequeira *et al.*, 1991; Olson and Sequeira, 1995). The individual-based models developed have successfully demonstrated a low-dimension system to exhibit chaotic behaviour (Stone, 1990) or spatial variability (Olson, 1995). Such individual-based approach in modelling was achieved by using object-oriented progamming (OOP).

In the individual-based model, each individual is modeled as an independent computer programme. The behaviour of each individual, including its interaction with each others, is specified within the entity itself. An "environment" is provided within which individuals interact with each other and their local environment. There is no overall controlling programme or agent in the model. The overall behaviour of the system can emerge from local interactions between independent agents.

One of the powerful aspects of individual-based models is that they can integrate many different levels in the traditional hierarchy of ecological processes (Huston *et al.*, 1988). Traditionally, each level of organization has been a separate field (e.g. population ecology, community ecology or ecosystem ecology), in which it has its own set of phenomena to explain. However, individual-based models demonstrate that all levels in this hierarchy can be understood by the interactions among individual organisms and their response to the environment.

Another important advantage of individual-based models over many state-variable models is that the properties of individual organisms and the mechanisms they employ to interact with their environment can be measured (Huston *et al.*, 1988). These kinds of data can be obtained from field studies, and thus can be easily incorporated into the models, making the models developed resembling the natural systems in a more realistic way.

By using individual-based approach in ecological modelling, the two basic tenets of biology mentioned before can thus be incorporated in the simulation. "Individuality" is permitted for each organism, since the properties of and the effects of interaction on each organism will not be averaged out. In addition, "locality" is allowed such that organisms can interact with other organisms and their environment locally within the model.

1.4 Hong Kong Marine Environment and Its Degradation

Hong Kong is situated on the southern coast of the People's Republic of China and lies between $22^0 9$'N to $22^0 7$'N, and $113^0 52$'E to $114^0 30$'E. Morton (1982) reviewed the basic hydrography of Hong Kong waters and indicated that in a global scale, Hong Kong inshore water is influenced by several water masses originating from different directions. These are Hainan current from south-western direction, Taiwan current from north-eastern direction and Kuroshio from eastern direction. These three oceanic currents have different ranges of water temperature and salinity and different times of dominance, and thus contribute to the variation of water temperature and salinity of Hong Kong waters throughout the year.

At a local level, Hong Kong is greatly influenced by the Pearl River, the major river of southern China. Hong Kong's territory water can be divided into three zones. As Hong Kong is located on the eastern bank of the Pearl River, its western borders are influenced to a very great degree by the discharge of fresh water from this river. Therefore, an estuarine environment is created on the western shore of Hong Kong. However, oceanic waters are dominantly influenced by Taiwan current and Kuroshio on the eastern shore with the Pearl River exerting little influence. The central region of Hong Kong is a zone of transition. In summer, as the flow of the Pearl River is increased by heavy rainfall, this transition zone is characterized by surface waters of reduced salinity, higher temperature and high dissolved oxygen content that flow over the more saline and cooler oceanic waters with low dissolved oxygen content. While in winter, water of this region is vertically homogenous as the flow from the Pearl River is reduced.

Hydrography therefore greatly influences the distribution of coral community in Hong Kong. As corals are sensitive to siltation (Riegl, 1995) and salinity (Coles and

Jokiel, 1978), the massive influence of the Pearl River, which brings in an enormous amount of fresh and silted water, makes the western shore of Hong Kong unsuitable for coral growth. However, as the oceanic current has dominant effect on the eastern shore of Hong Kong and there is little influence from the Pearl River, coral communities can develop there. A survey done in the early 80's showed the major areas of coral growth in Hong Kong to start from its southern end around Lamma Island up to the north-eastern end around Ping Chau (Scott, 1984).

However, degradation of present marine and coastal environment of Hong Kong can be observed everywhere. Beginning in the late 1970's, large area of the eastern coastal zone of Hong Kong has been filled up for land reclamation, thus destroying a lot of coral reefs there. In addition, since the early 1990's, due to the Airport Core Programme (ACP) project, large numbers of dumping and dredging sites were established in Hong Kong marine environment. The increase of siltation in the water body brought about by dumping and dredging decreases the chance of survival of the coral community. A significant decrease in coral diversity and coral cover has already been observed along the Tolo Channel within a fifthteen-year period (Scott and Cope, 1988; Cheung, unpublished data). Therefore, there is an urgent need to protect and conserve these delicate coral communities.

1.5 Objectives of the Present Study

The objectives of the present study are to evaluate the diversity of the coral community in Ping Chau, an island on the north eastern part of Hong Kong. An object-oriented computer model will then be developed to simulate the dynamics of this coral community. The response of the community to disturbance will be investigated based on the model developed. Actual field information will be compared with the results generated from the model. From the overall results generated, mechanisms governing the dynamical behaviour of a complex ecological community may be better understood. The results obtained from the modelling exercise can hopefully be used to develop a programme for the conservation of coastal environments in Hong Kong in the future.

CHAPTER 2 FIELD STUDIES OF A CORAL COMMUNITY IN HONG KONG

2.1 Introduction

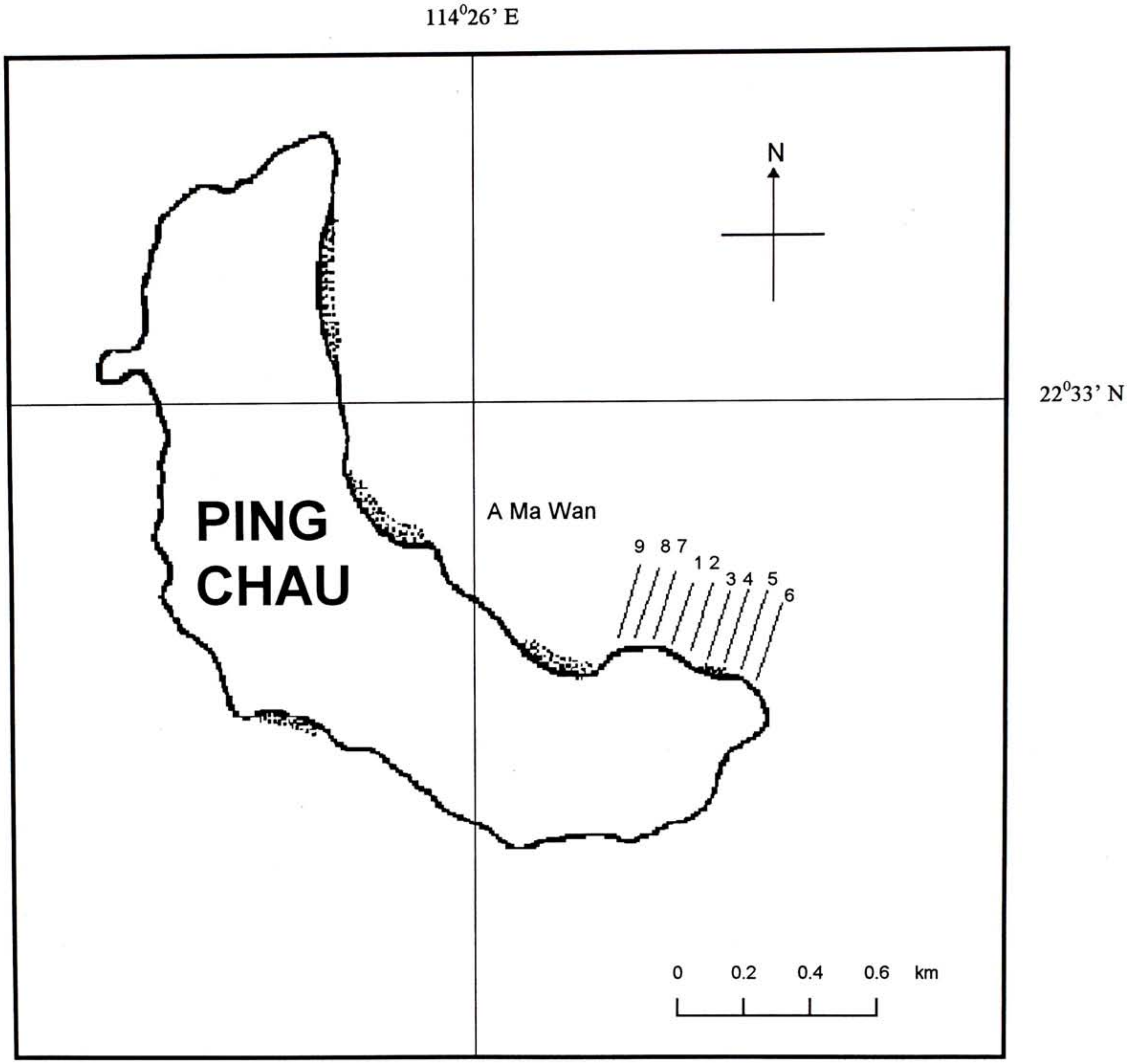
The Hong Kong coral community was surveyed in the 1980s (Scott and Cope, 1982; Veron, 1982) and found to occur mainly in the south-eastern to north-eastern side of Hong Kong (Scott, 1984). Earlier studies showed that in the north-eastern side, the reef was dominated by hermatypic corals, while in the south-eastern side it was dominated by ahermatypic corals (Scott, 1984). Further studies were conducted mainly along the eastern coastline of Hong Kong (Cope and Morton, 1988; Scott and Cope, 1988). A remote island, Ping Chau, which is situated in the north-eastern part of Hong Kong, received little attention. Only one published record has been made for the coral community in one selected site of Ping Chau (Morton and Morton, 1983). In addition, because of its remoteness, Ping Chau is spared from the serious impact of marine pollution occurring in the other coastal environment of Hong Kong (e.g. water pollution due to industrial and domestic waste, siltation from dredging and dumping event). The marine environment of Ping Chau is thus one of the best remaining marine environments in Hong Kong. Understanding the coral community structure of Ping Chau becomes an urgent task in order to conserve what may probably be the best coral community left in Hong Kong.

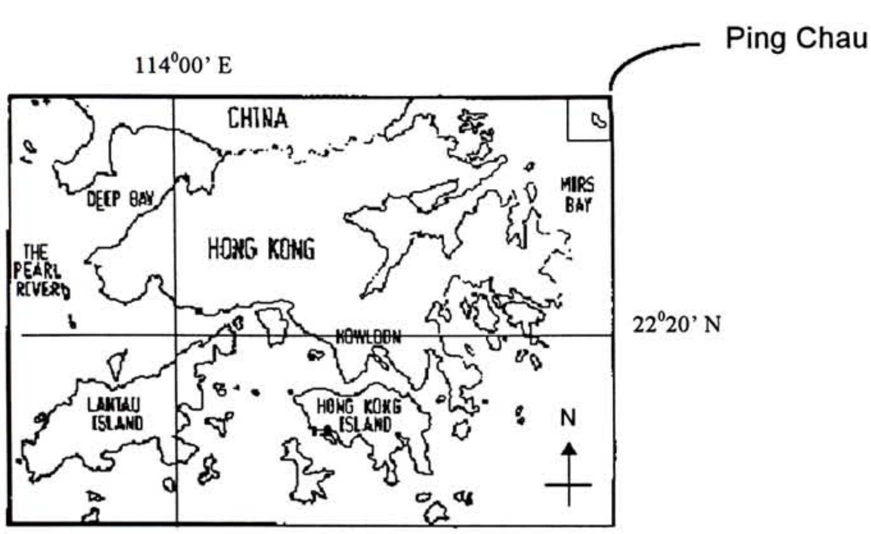
This chapter presents the results of field surveys on a coral community in Ping Chau. A preliminary quantitative survey was first conducted in March and April of 1996 to identify the pre-dominant growth forms of scleractinian corals in the study site. These results were incorporated in the modelling study (Chapter 3). An extensive field survey was subsequently carried out from January to April, 1997 to obtain a more complete picture of the coral community structure in the selected site. This extensive survey generated significant field samples that were used to verify results from the simulation model developed in this research (see Chapters 3 and 4). In addition, this field survey provides the first-hand data that serves as part of the long-term monitoring programme of the coral reef community in the study site.

2.2 Study Area

Ping Chau is an outlying island in the northeasternmost part (114°26'E, 22°33'N) of Hong Kong (Figure 2.1). The study area was a coral reef situated to the south-eastern end of the island near a beach called A Ma Wan. The area was chosen because it is the largest and probably the best coral community found in the island. Water depth of the study area ranges from 0 to -3 m CD. The shallow water zone of the reef area (0 to -2 m CD) is mainly composed of rocky substratum, while the deeper end of it (-1 m to -3 m CD) is mainly composed of rocky-sandy bottom. There is a distinct central sandy channel that divides the shallow water zone of the study area into left and right sections with rocky substratum. The area to the right of the central sandy channel was more exposed to wave action than the rest of the study area.

Figure 2.1. Map of Ping Chau showing the location of the permanent transects.


114°26' E
22°33' N
N
PING
CHAU
A Ma Wan
9 8 7
1 2
3 4 5
6
0 0.2 0.4 0.6 km


Ping Chau
114°00' E
22°20' N
CHINA
DEEP BAY
MIRS BAY
THE PEARL RIVER
HONG KONG
KOWLOON
LANTAU ISLAND
HONG KONG ISLAND
N

2.3. Materials and Methods

2.3.1 Preliminary Study of the Coral Cover and Diversity

A preliminary survey was carried out by continuous transect recording (CTR) method (Loya, 1978). Five 25-m transect lines were randomly laid down from the shore to seaward side of the reef area. All corals crossed by the transect were identified and their length covered by the transects recorded. Coral identification was based on the key provided by Veron (1993).

Quadrat-area method was also conducted for the preliminary study. A 0.5m x 0.5m quadrat was placed and coral cover recorded by underwater video camera at 5m-point, 10m-point and 25-m point along each transect (set out in connection with the CTR method mentioned earlier). The quadrat used was equally divided into 25 10cm x 10cm small squares, and a close-up recording of each square was done each time when video-taking so as to increase the resolution of the pictures taken for later coral cover measurement in the computer. All coral species within each quadrat were identified and their area cover measured from the video using an image analyzer. The results obtained from the quadrat-area method were compared with results generated from CTR method to get a better picture of the dominant coral groups in the study area.

2.3.2 Extensive Study of the Coral Cover and Diversity

Nine 40m-long permanent transects were laid down perpendicular to the shore of the study area (Figure 2.1) over a period from January to April, 1997. The first transect was laid down at a random location in the middle part of the study area. Subsequent transects established and were numbered in the following sequence from left to right: 7, 8, 9, 1, 2, 3, 4, 5 and 6.Transects 7, 8, 9 and 1 were found situated left to the central sandy channel of the study area, while transects 5 and 6 were located right to it. The remaining transects (2 to 4) were situated in the central sandy channel. All transects started at point zero of chart datum and were 10 meters apart parallel to each other. The total area covered by the transects was about 3,600 m^2. Two pegs were fixed at 2m intervals along each transect. Additional pegs were fixed at 5m intervals. The pegs were labelled and were used as the permanent markers for the long-term monitoring study of the area.

Quadrat-area method described in Section 2.3.1 was also used in this survey. A quadrat with a size of 0.5m x 0.5m, and divided into 25 10cm x10cm squares, was placed at every 5m-interval along each permanent transect and the coral cover of each square within the quadrat recorded by underwater video camera. Seventy-nine quadrats with a total area of 19.75 m^2 were surveyed. All corals within each quadrat were identified and their area cover measured by an image analyzer on the picture recorded in the video tape.

2.3.3 Relative Abundance and Species Diversity

Relative abundance was used to compare the dominance of each coral species and to provide information on the composition of coral species in the community, while Brillouin Index (Brower *et al.*, 1989) was used to characterize the species diversity recorded. Relative abundance of each coral species was measured as the percentage of its length cover over the total length cover (CTR method) or its area cover over the total area covered (Quadrat-area method). As non-random sampling was employed in this survey, the use of Brillouin Index was suggested by Brower *et.al.* (1990) for statistical comparison between the coral communities of different parts of the study area. The equation of Brillouin Index is given as:

$$\boldsymbol{H} = (\log N\,! - \Sigma \log n_i!) \,/\, N$$

where n_i is the area covered by species i in cm (CTR method), or in cm^2 (Quadrat-area method) and N is the total length covered (CTR method), or total area covered (Quadrat-area method) by all species found. One cm of length cover (CTR method) or one cm^2 of area cover (Quadrat-area method) was considered as an “individual” in the study.

2.4 Results and Discussion

2.4.1 Preliminary Study

Seventeen hermatypic scleractinian coral species with a 46.49% total coral cover were recorded by CTR method, while 14 species and 50.77% total coral cover were recorded by using the quadrat-area method (Figures 2.2). The Brillouin Index obtained by CTR and quadrat-area method was 0.9199 and 0.9160 respectively. *Platygyra sinensis* was the dominant species recorded by both methods. It has also been identified as the common shallow water species in Hong Kong (Cope and Morton, 1988). Both these methods showed similar results on the coral community structures of the study area.

After re-grouping, five dominant groups of corals of different growth forms were identified from both the CTR and quadrat-area methods in the preliminary survey. These were massive-form or castle-like corals of Family Faviidae, foliaceous *Pavona decussata* of Family Agariciidae, branching or tabular form corals of Family Acroporidae, mushroom-like corals with elongated polyps (belonging to genus *Goniopora* or *Alveopora* of Family Poritidae) and massive-form *Porites lobata* of Family Poritidae (Figures 2.3). These five groups of coral are known to have their own distinct biological characteristics, competitive mechanisms and response to environmental changes and different types of disturbance (Kinsman, 1964; Woodley *et al.*, 1981; Hughes and Jackson, 1985; Lang and Chornesky, 1990; Sorokin, 1993).

Corals of Family Acroporidae are usually fast-growing and opportunistic. Their growth form is usually ramose or tabular. They are very sensitive to temperature change and will achieve an optimal growth only when the temperature is suitable. They are also sensitive to physical disturbance. It was recorded that up to 99% of acroporids in shallow water zone (0 m - 10 m) was damaged in a single strong hurricane that occurred in Jamaica (Woodley *et al.*, 1981).

Species of *Pavona* are also considered as fast-growing and opportunistic corals, but their growth rate is not as fast as that of acroporids. Their growth form is usually foliaceous and such growth form of corals was found to have high survivorship under hurricane impact (Hughes and Jackson, 1985). Histoincompatibility was known to be used by *Pavona* sp. for competition. However, corals with such growth form have not been found to use overgrowth mechanism to grow over other corals (Land and Chornesky, 1990).

Corals of Family Faviidae are slow-growing and are k-strategists. They were considered to be less sensitive to environmental changes (Sorokin, 1993). Their body forms are usually massive, castle-like or encrusting. Because of their growth form, they were found able to withstand physical disturbance (just about 9% of them being damaged in the hurricane described by Woodley *et al.*, 1981). This group of corals usually have aggressive killing activities brought about by their sweeper tentacles or mesenterial filaments during interspecific competition (Land and Chornesky, 1990).

Corals of Family Poritidae are also slow-growing. Similar to faviids, they can adapt to a wide range of environmental conditions. *Porites* group of this family even has been demonstrated to be very tolerant to sub-lethal range of environmental conditions (Kinsman, 1964; Coles *et al*, 1976). The growth form of *Porites* sp. is usually massive, while that of *Goniopora* sp. or *Alveopora* sp. is usually mushroom-like. However, members of this family show a large variation in their competitive mechanisms. Genus *Goniopora* or *Alveopora* of this family uses a very aggressive killing mechanism by its elongated sweeper polyps during competition (Lang and Chornesky, 1990). In contrast, *Porites lobata* was considered to be the least aggressive coral in the hierarchy model developed by Cope (1982).

Figure 2.2. Relative abundance of coral species recorded in the preliminary study of the coral community at A Ma Wan, Ping Chau by continuous transect recording method (CTR method) and Quadrat-area method (February to April, 1996).

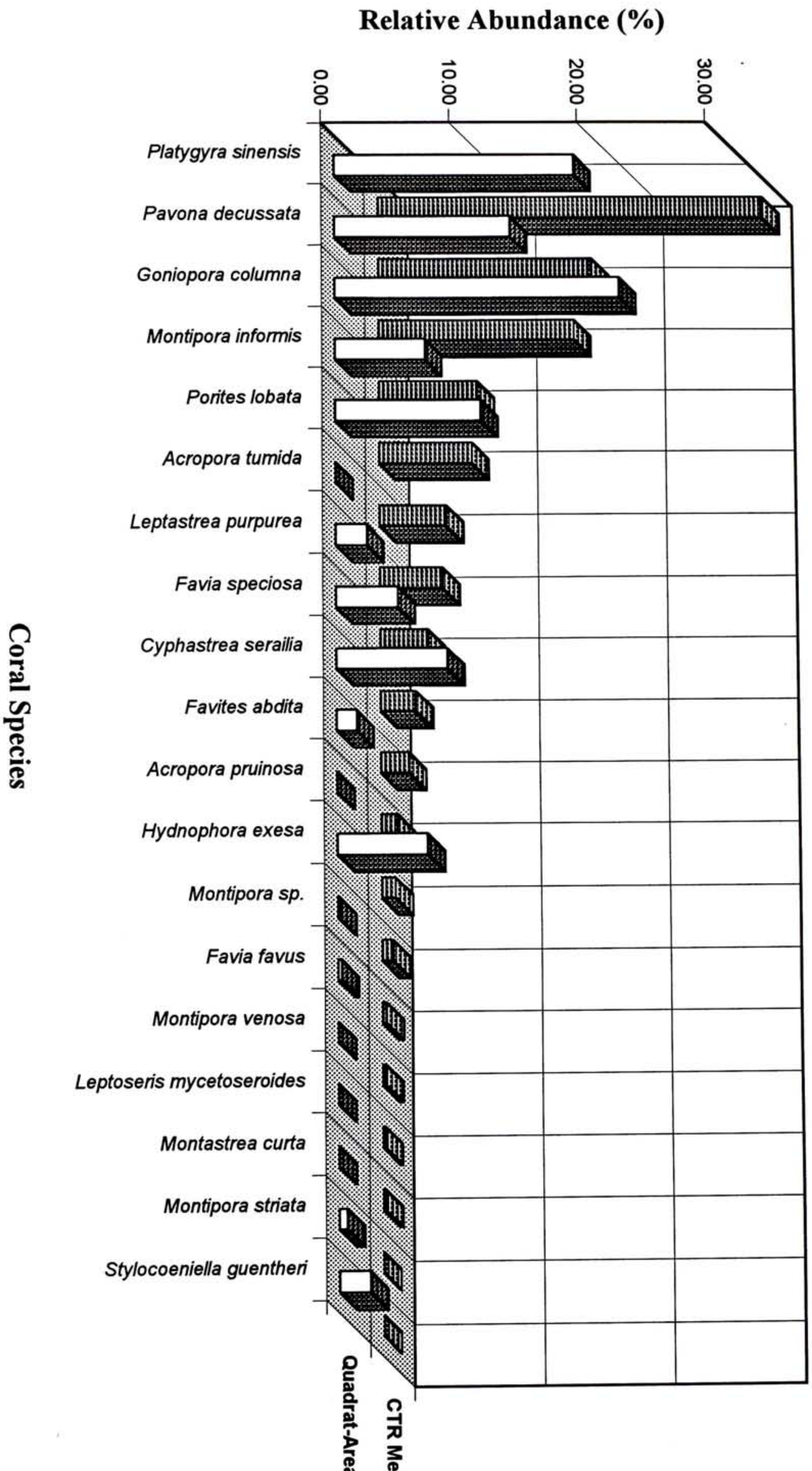
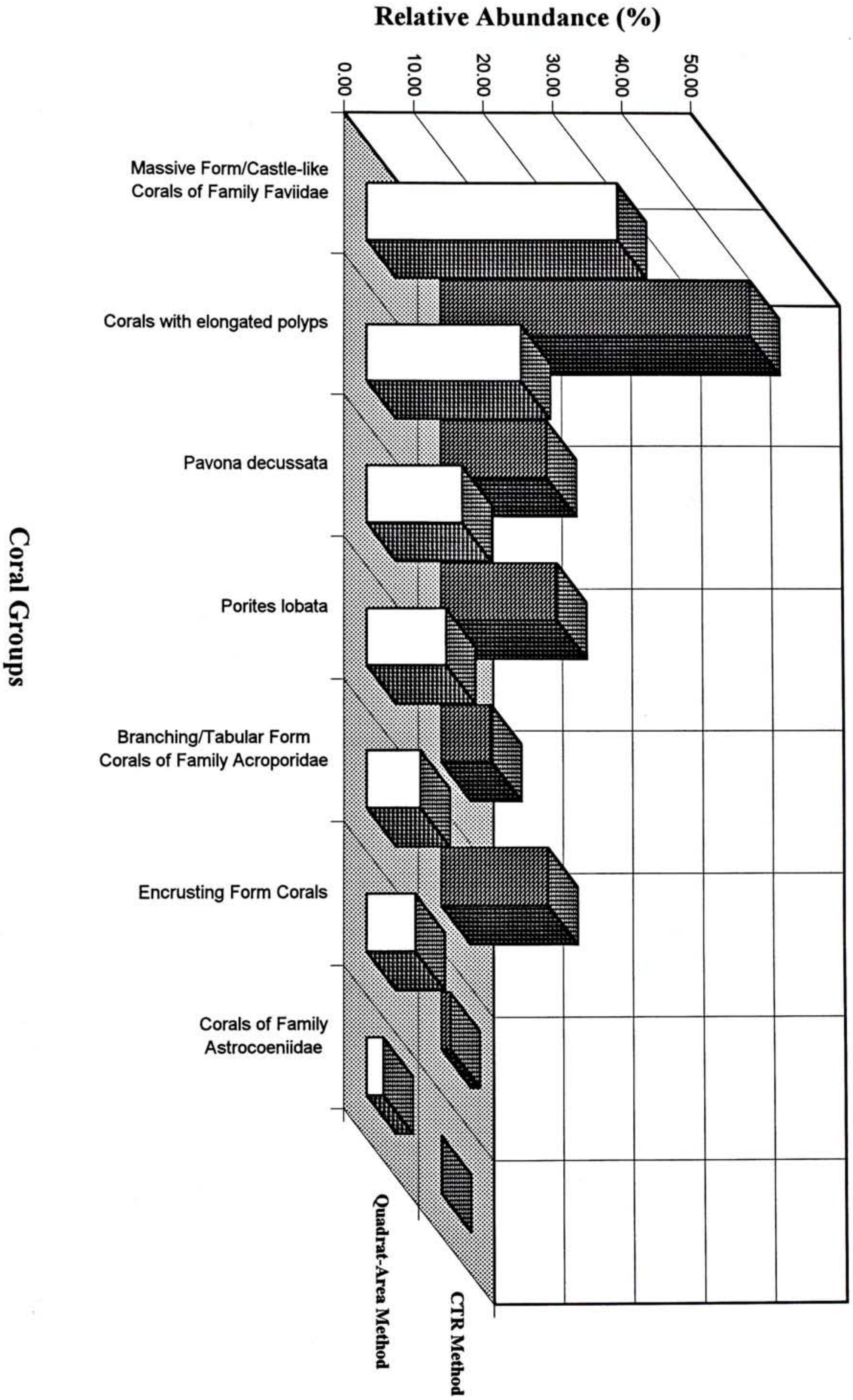

Relative Abundance (%)
0.00
10.00
20.00
30.00
Coral Species
Platygyra sinensis
Pavona decussata
Goniopora columna
Montipora informis
Porites lobata
Acropora tumida
Leptastrea purpurea
Favia speciosa
Cyphastrea serailia
Favites abdita
Acropora pruinosa
Hydnophora exesa
Montipora sp.
Favia favus
Montipora venosa
Leptoseris mycetoseroides
Montastrea curta
Montipora striata
Stylocoeniella guentheri
CTR Method
Quadrat-Area Method

Figure 2.3. Relative abundance of the coral groups recorded in the preliminary study of the coral community at A Ma Wan, Ping Chau by continuous transect recording method (CTR method) and Quadrat-area method (February to April, 1996).



Relative Abundance (%)
0.00
10.00
20.00
30.00
40.00
50.00
Massive Form/Castle-like Corals of Family Faviidae
Corals with elongated polyps
Pavona decussata
Porites lobata
Branching/Tabular Form Corals of Family Acroporidae
Encrusting Form Corals
Corals of Family Astrocoeniidae
Coral Groups
CTR Method
Quadrat-Area Method

2.4.2 Extensive Study

2.4.2.1 Coral Diversity and Area Cover

Twenty-five hermatypic scleractinian coral species of nine families were identified in this study and were listed in Table 2.1. Percentage of coral cover of each quadrat ranged from 0-100%. Total coral cover was 51.82% and the overall Brillouin Index calculated was 1.021. *Goniopora columna, Montipora informis, Pavona decussata, Platygyra sinensis* and *Porites lobata* were the five dominant species found. Among the corals identified, *Platygyra sinensis* was the most dominant species with about 26% relative abundance (Figure 2.4). These five coral species were also the representative species of the five dominant coral groups identified in the preliminary study.

2.4.2.2 Zonation of Coral Community in the Study Area

Zonation of coral community structure has been known for a few decades. Coral zonation has been found to be determined by the integrated effects of physical disturbance, environmental conditions and biological interactions within the coral community (Connell, 1973; Done, 1982; Lang and Chornesky, 1990; Sorokin, 1993; Lirman and Fong, 1996). Since the area covered by this present study was about 3,600 m^2, such an area was considered large enough to allow different degrees of physical disturbance to occur within. Different parts of the study area could be subjected to different degrees of physical disturbance brought about by tidal waves and storm during typhoon season. In addition, as there was a distinct qualitative differentiation of the type of substratum in the study area - left and right shallow water zones were mainly rocky while the remaining area has sandy bottom, different parts of the study area may be subjected to different degrees of siltation. As scleractinian corals are sensitive to the effect of siltation (Riegl, 1995), exposure to different degrees of siltation could affect the species composition of different zones within the area.

Table 2.1. List of corals recorded in the extensive field study of the coral community at A Ma Wan, Ping Chau (January to April, 1997).

Family Acroporidae Verrill, 1902
- *Acropora tumida* Verrill, 1866
- *Montipora informis* Bernard, 1897
- *Montipora sp.*

Family Agariciidae Gary, 1847
- *Pavona decussata* (Dana, 1846)

Family Astrocoeniidae Koby, 1890
- *Stylocoeniella guentheri* Bassett-Smith, 1890

Family Dendrophylliidae Gray, 1847
- *Turbinaria peltata* (Esper, 1794)

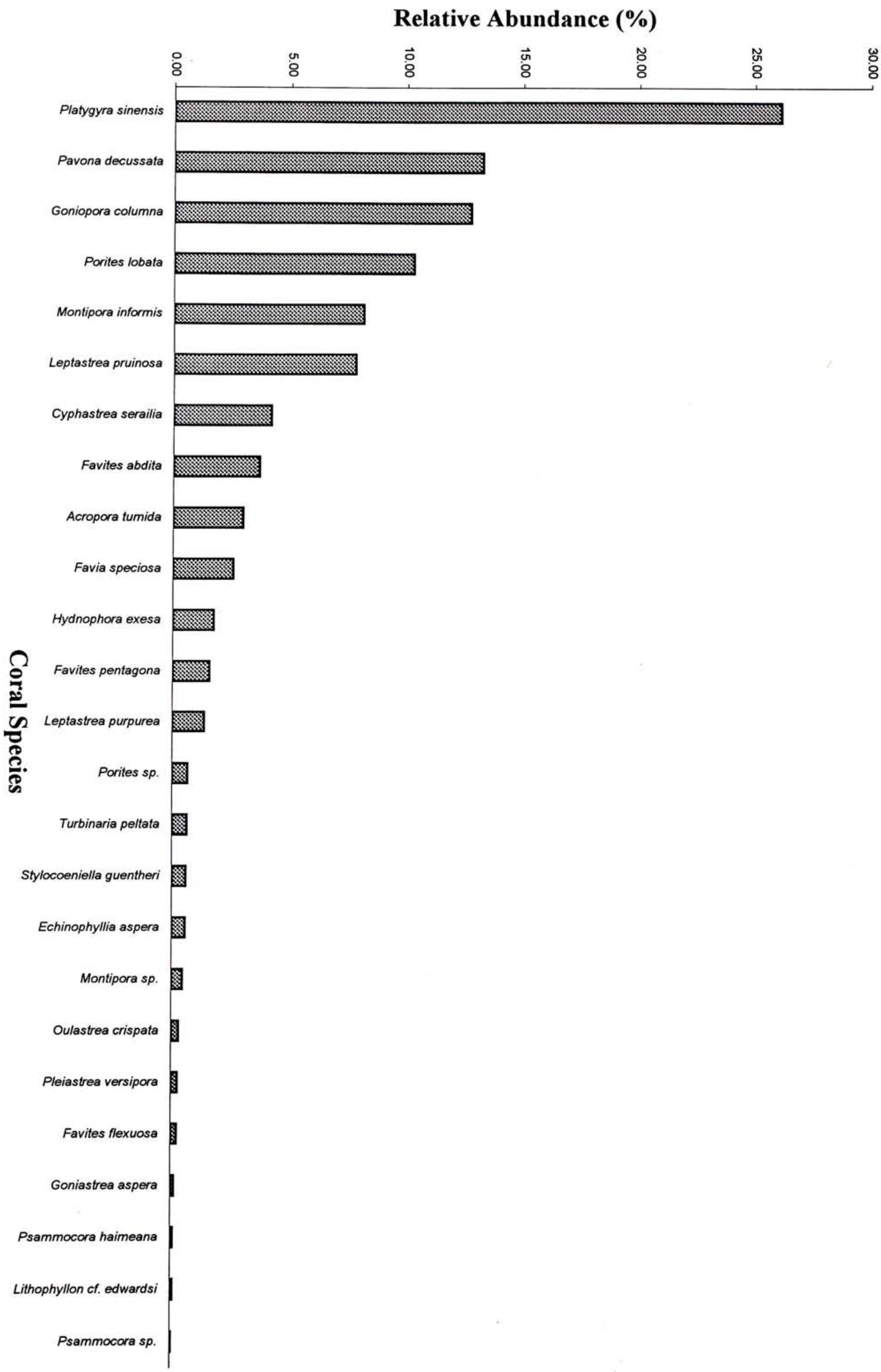
Family Faviidae Gregory, 1900
- *Cyphastrea serailia* (Forskål, 1775)
- *Favia speciosa* (Dana, 1846)
- *Favites abdita* (Ellid and Solander, 1786)
- *Favites flexuosa* (Dana, 1846)
- *Favites pentagona* (Esper, 1794)
- *Goniastrea aspera* (Verrill, 1865)
- *Hydnophora exesa* (Pallas, 1766)
- *Leptastrea pruinosa* Crossland, 1952
- *Leptastrea purpurea* (Dana, 1846)
- *Lithophyllon* cf. *edwardsi* (Rosseau, 1854)
- *Oulastrea crispata* (Lamarck, 1816)
- *Platygyra sinensis* (Edwards and Haime, 1849)
- *Pleiastrea versipora* (Lamarck, 1816)

Family Pectiniidae Vaughan & Wells, 1943
- *Echinophyllia aspera* (Ellis & Solander, 1786)

Family Poritidae Gray, 1842
- *Goniopora columna* Dana, 1846
- *Porites lobata* Dana, 1846
- *Porites sp.*

Family Thamnasteriidae Vaughan & Wells, 1943
- *Psammocora haimeana* Edwards & Haime, 1851
- *Psammocora* sp.

Figure 2.4. Relative abundance of coral species recorded in the extensive field study of the coral community at A Ma Wan, Ping Chau (January to April, 1997).



Relative Abundance (%)
0.00
5.00
10.00
15.00
20.00
25.00
30.00
Coral Species
Platygyra sinensis
Pavona decussata
Goniopora columna
Porites lobata
Montipora informis
Leptastrea pruinosa
Cyphastrea serailia
Favites abdita
Acropora tumida
Favia speciosa
Hydnophora exesa
Favites pentagona
Leptastrea purpurea
Porites sp.
Turbinaria peltata
Stylocoeniella guentheri
Echinophyllia aspera
Montipora sp.
Oulastrea crispata
Pleiastrea versipora
Favites flexuosa
Goniastrea aspera
Psammocora haimeana
Lithophyllon cf. edwardsi
Psammocora sp.

In order to investigate the possibility of coral zonation in the study area, the study area was divided into six zones with respect to their potential exposure to different degrees of physical disturbance. Each zone defined was covered by parts of the permanent transects established (Figure 2.5). Total coral cover, number of species, relative abundance of each coral species and the Brillouin Index were then re-calculated for each zone (Table 2.2 and Figures 2.6 - 2.11).

Variations in coral community structure were observed in the six zones defined. Zone 1 (left shallow rocky zone) has the highest percentage of total coral cover and the highest number of coral species. The composition and relative abundance of the five dominant species also showed distinct differences among the different zones (Figure 2.12). For example, *Montipora informis* was found dominant only in Zones 2 (left deep sandy zone) and 4 (middle deep sandy zone), but was totally absent in Zone 5 (right shallow rocky zone).

The different relative abundances of the five dominant species among the different zones provide the first evidence of zonation pattern found in the coral community studied. *Goniopora columna*, which is a coral species with elongated polyps (Section 2.4.1), was found to be dominant only in Zone 6 (right deep sandy zone) (Figure 2.12). Possession of elongated polyps allows *G. columna* to clear the sediment deposited on its coral colony more efficiently than those species without elongated polyps. Since all the dominant species found in other zones did not possess elongated polyps, the specific dominance of *G. columna* in Zone 6 might indicate that Zone 6 was frequently subjected to siltation disturbance. Hence, only the siltation-resistant species like *G. columna* could survive in that zone.

Such observation may further be supported by the physical location of Zone 6 in the study area. Zone 6 was situated in a relatively more exposed area (Section 2.2) when compared with the other deep water zones. Larger amount of sediment could be stirred up by stronger waves, hence corals found there could be subjected to more frequent siltation disturbance.

Similar interpretation could be applied to the specific dominance of *Platygyra sinensis* in shallow water zones (Zones 1, 3, 5, Figures 2.5 and 2.12). As colonies of *P. sinensis* observed in the study area were usually large, heavy and castle-like, such colony form could withstand stronger wave stress. Dominance of *P. sinensis* in shallow water zones thus implied that these zones were frequently subjected to strong wave stress. As shallow water zones were nearer to the shore, stronger wave and storm stresses were more likely to occur in here than in the deeper water zones (i.e., Zones 2, 4, 6, Figure 2.5).

The storm-sensitive coral species, *Pavona decussata* and *Montipora informis* (Section 2.4.1) were found dominant in Zone 2 (left deep sandy zone) and Zone 4 (middle deep sandy zone) respectively. Since these two species were more vulnerable to storm disturbance than did *P. sinensis* and *G. columna*, their dominance might indicate that Zones 2 and 4 had a relatively more stable environment. The dominance of these two species in stable environment was due to their fast-growing habit. Such habit has been identified as one of the strategies for a coral to gain dominance in a coral community (Sorokin, 1993).

Figure 2.5 Distribution of the permanent transects and the six zones defined for the study area at A Ma Wan, Ping Chau.

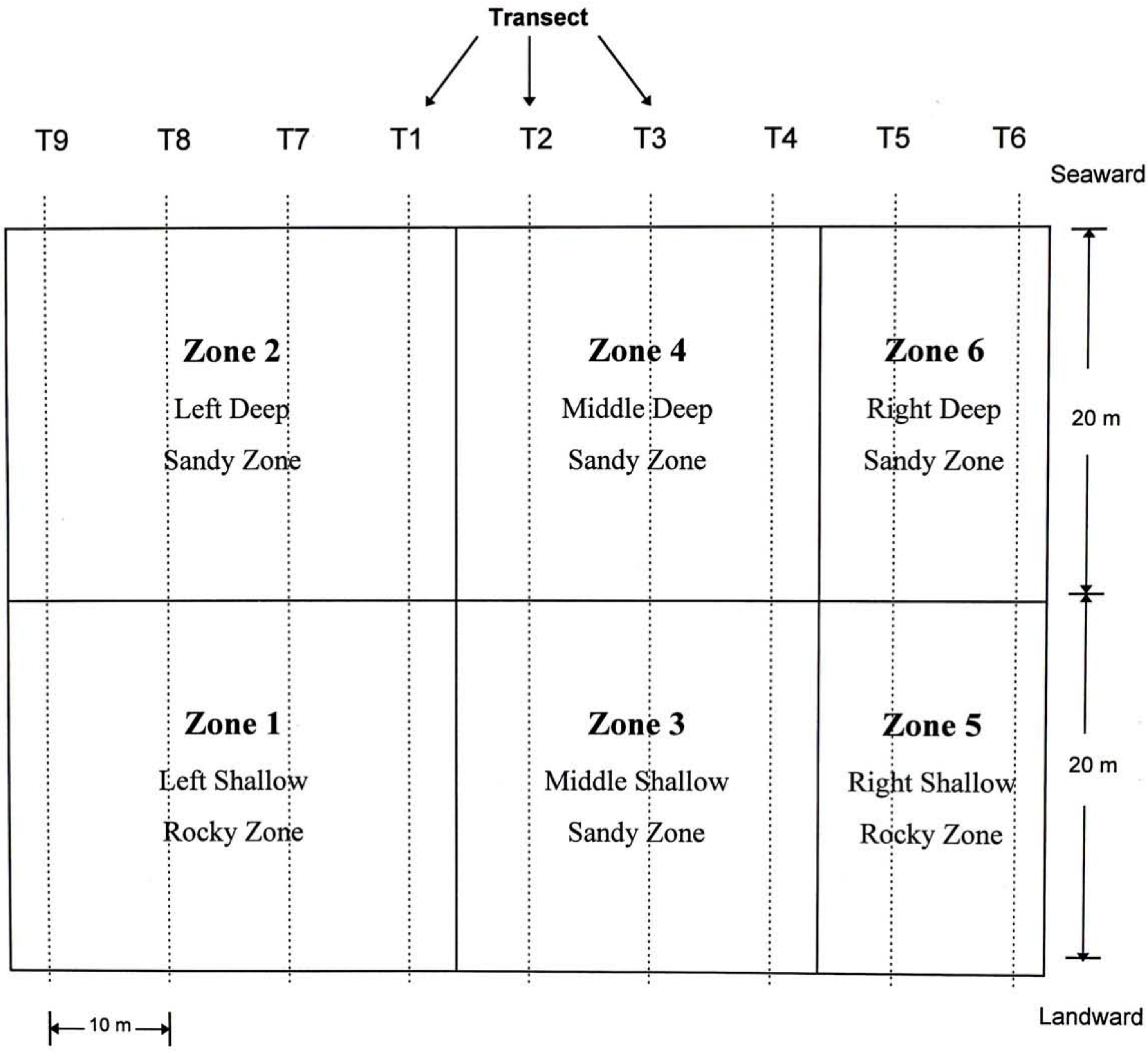
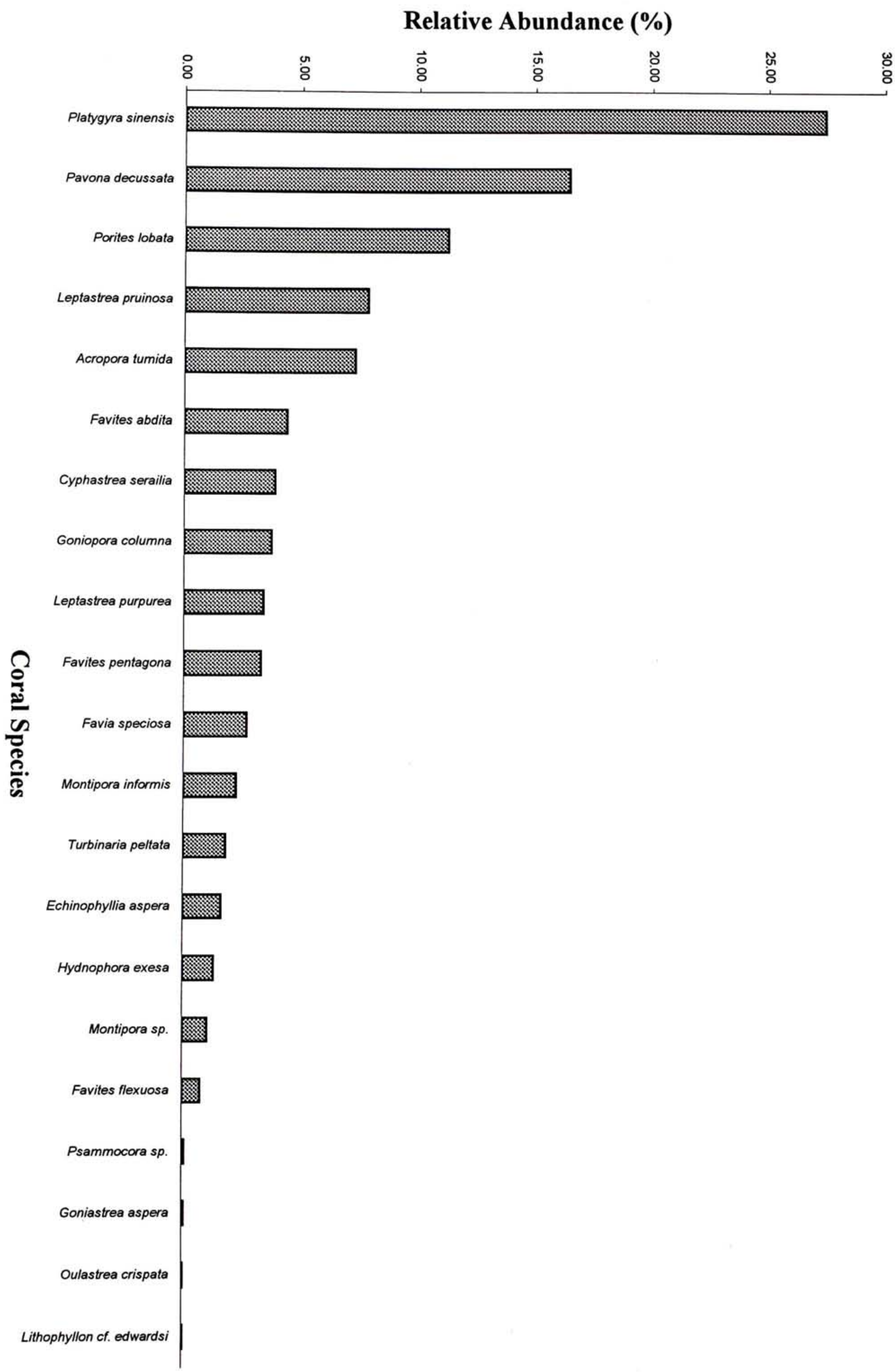

Transect
T9
T8
T7
T1
T2
T3
T4
T5
T6
Seaward
Zone 2
Left Deep
Sandy Zone
Zone 4
Middle Deep
Sandy Zone
Zone 6
Right Deep
Sandy Zone
20 m
Zone 1
Left Shallow
Rocky Zone
Zone 3
Middle Shallow
Sandy Zone
Zone 5
Right Shallow
Rocky Zone
20 m
10 m
Landward

Table 2.2. The total coral cover, species richness and mean Brillouin Index of diversity of the scleractinian coral community found in the six defined zones described in Figure 2.5.

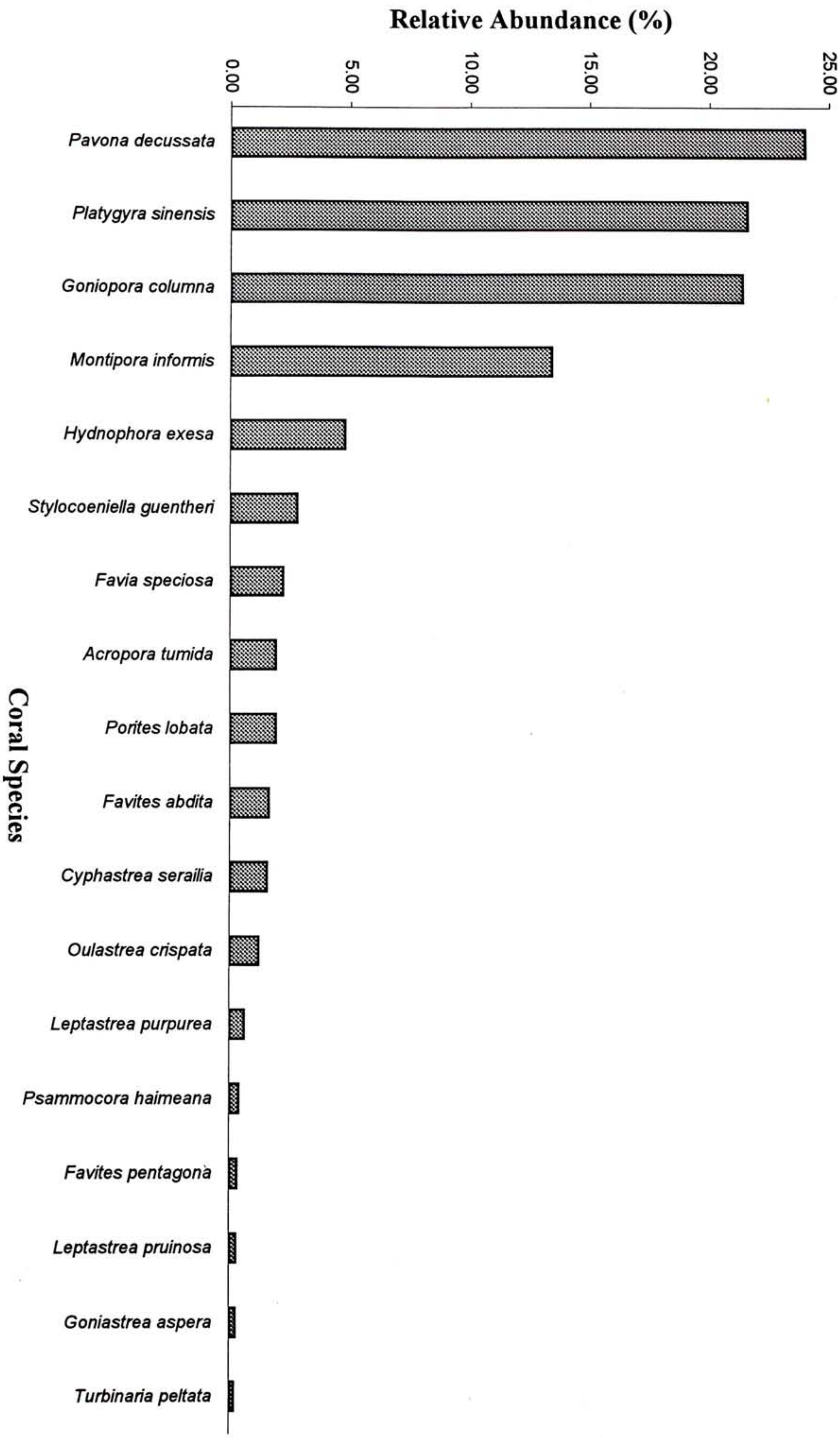
Zone No.	Zone Description	Total Coral Cover (%)	Number of Species	Mean Brillouin Index
1	Left shallow rocky zone	63.10	21	0.4722
2	Left deep sandy zone	54.67	18	0.3661
3	Middle shallow sandy zone	42.98	18	0.2906
4	Middle deep sandy zone	45.02	12	0.3634
5	Right shallow rocky zone	48.48	12	0.5674
6	Right deep sandy zone	48.94	12	0.3805

Figure 2.6. Relative abundance of coral species found in Zone 1 (left shallow rocky zone) of the study area at A Ma Wan, Ping Chau.



Relative Abundance (%)
0.00
5.00
10.00
15.00
20.00
25.00
30.00
Coral Species
Platygyra sinensis
Pavona decussata
Porites lobata
Leptastrea pruinosa
Acropora tumida
Favites abdita
Cyphastrea serailia
Goniopora columna
Leptastrea purpurea
Favites pentagona
Favia speciosa
Montipora informis
Turbinaria peltata
Echinophyllia aspera
Hydnophora exesa
Montipora sp.
Favites flexuosa
Psammocora sp.
Goniastrea aspera
Oulastrea crispata
Lithophyllon cf. edwardsi

Figure 2.7. Relative abundance of coral species found in Zone 2 (left deep sandy zone) of the study area at A Ma Wan, Ping Chau.



Relative Abundance (%)
0.00
5.00
10.00
15.00
20.00
25.00
Coral Species
Pavona decussata
Platygyra sinensis
Goniopora columna
Montipora informis
Hydnophora exesa
Stylocoeniella guentheri
Favia speciosa
Acropora tumida
Porites lobata
Favites abdita
Cyphastrea serailia
Oulastrea crispata
Leptastrea purpurea
Psammocora haimeana
Favites pentagona
Leptastrea pruinosa
Goniastrea aspera
Turbinaria peltata

Figure 2.8. Relative abundance of coral species found in Zone 3 (middle shallow sandy zone) of the study area at A Ma Wan, Ping Chau.

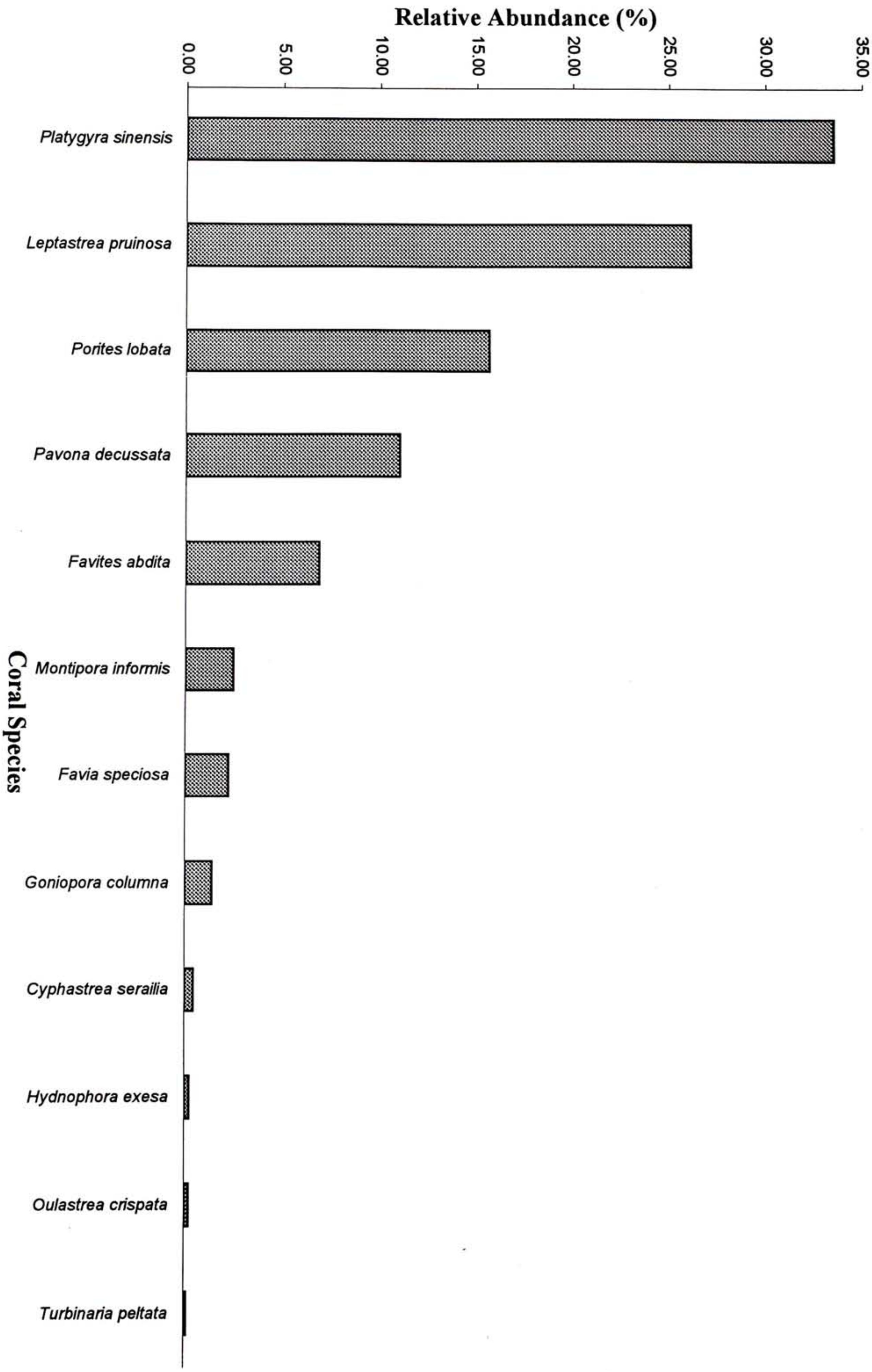

Relative Abundance (%)
0.00
5.00
10.00
15.00
20.00
25.00
30.00
35.00
Coral Species
Platygyra sinensis
Leptastrea pruinosa
Porites lobata
Pavona decussata
Favites abdita
Montipora informis
Favia speciosa
Goniopora columna
Cyphastrea serailia
Hydnophora exesa
Oulastrea crispata
Turbinaria peltata

Figure 2.9. Relative abundance of coral species found in Zone 4 (middle deep sandy zone) of the study area at A Ma Wan, Ping Chau.

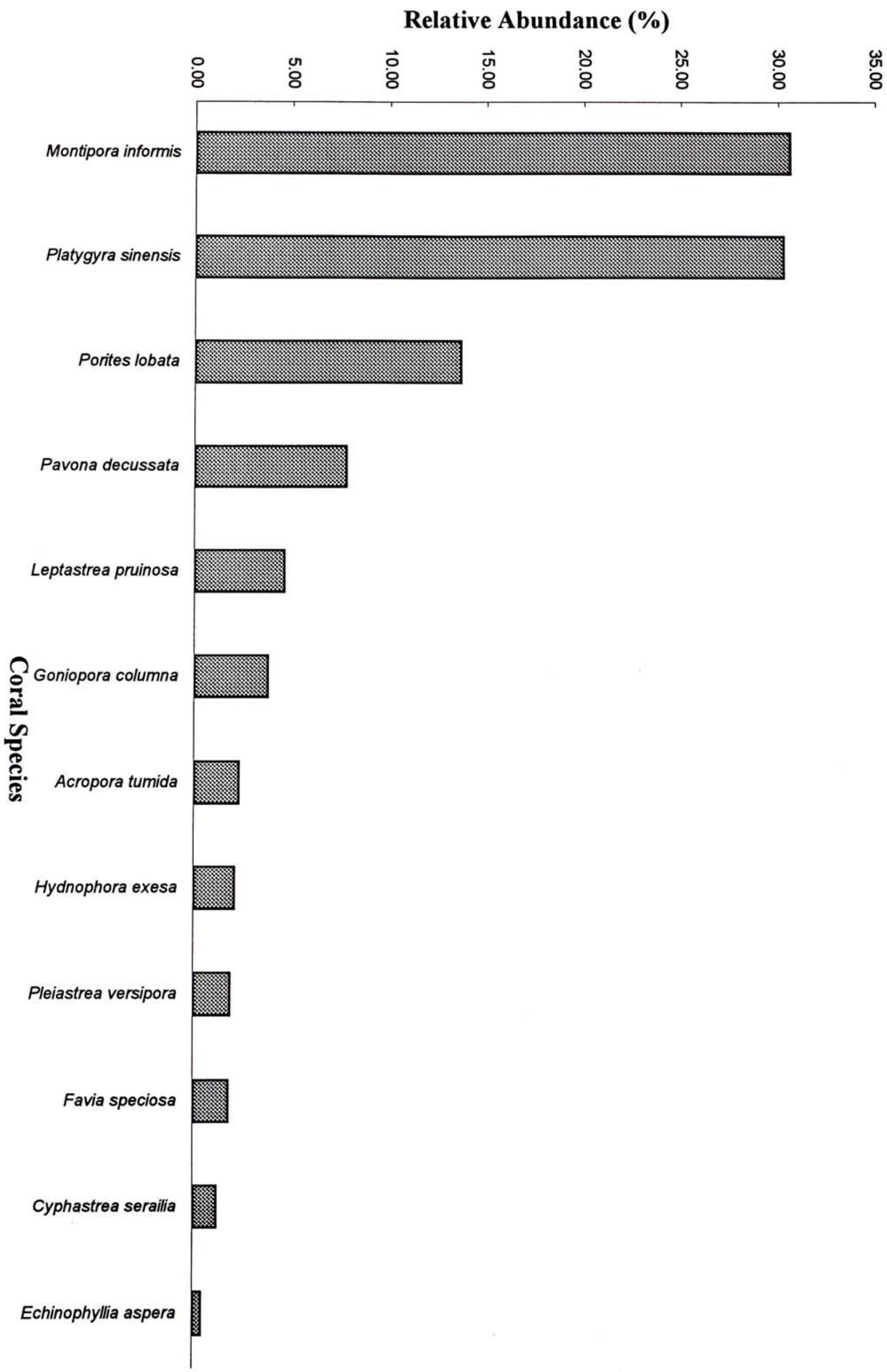

Relative Abundance (%)
0.00
5.00
10.00
15.00
20.00
25.00
30.00
35.00
Coral Species
Montipora informis
Platygyra sinensis
Porites lobata
Pavona decussata
Leptastrea pruinosa
Goniopora columna
Acropora tumida
Hydnophora exesa
Pleiastrea versipora
Favia speciosa
Cyphastrea serailia
Echinophyllia aspera

Figure 2.10. Relative abundance of coral species found in Zone 5 (right shallow rocky zone) of the study area at A Ma Wan, Ping Chau.

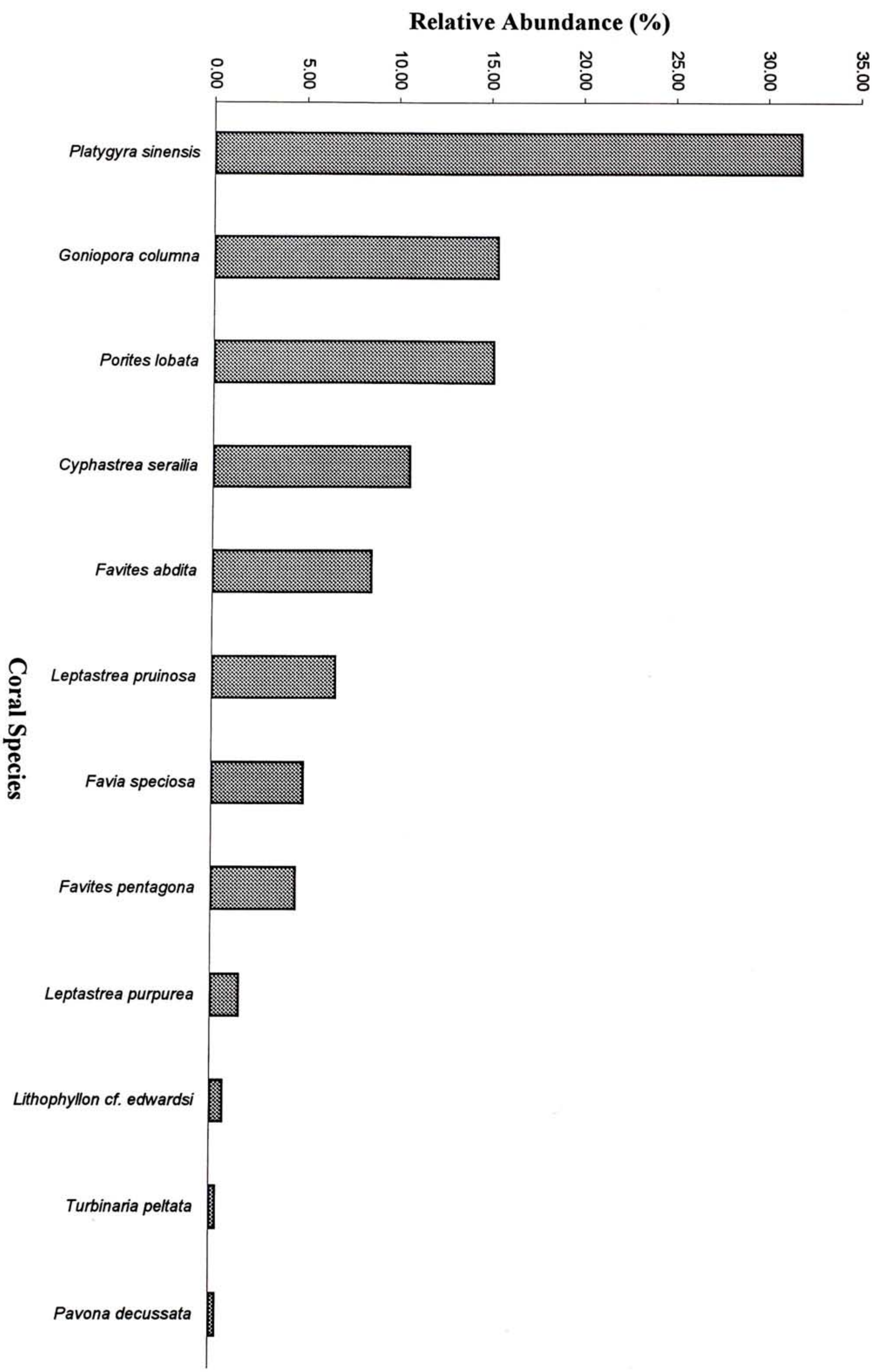
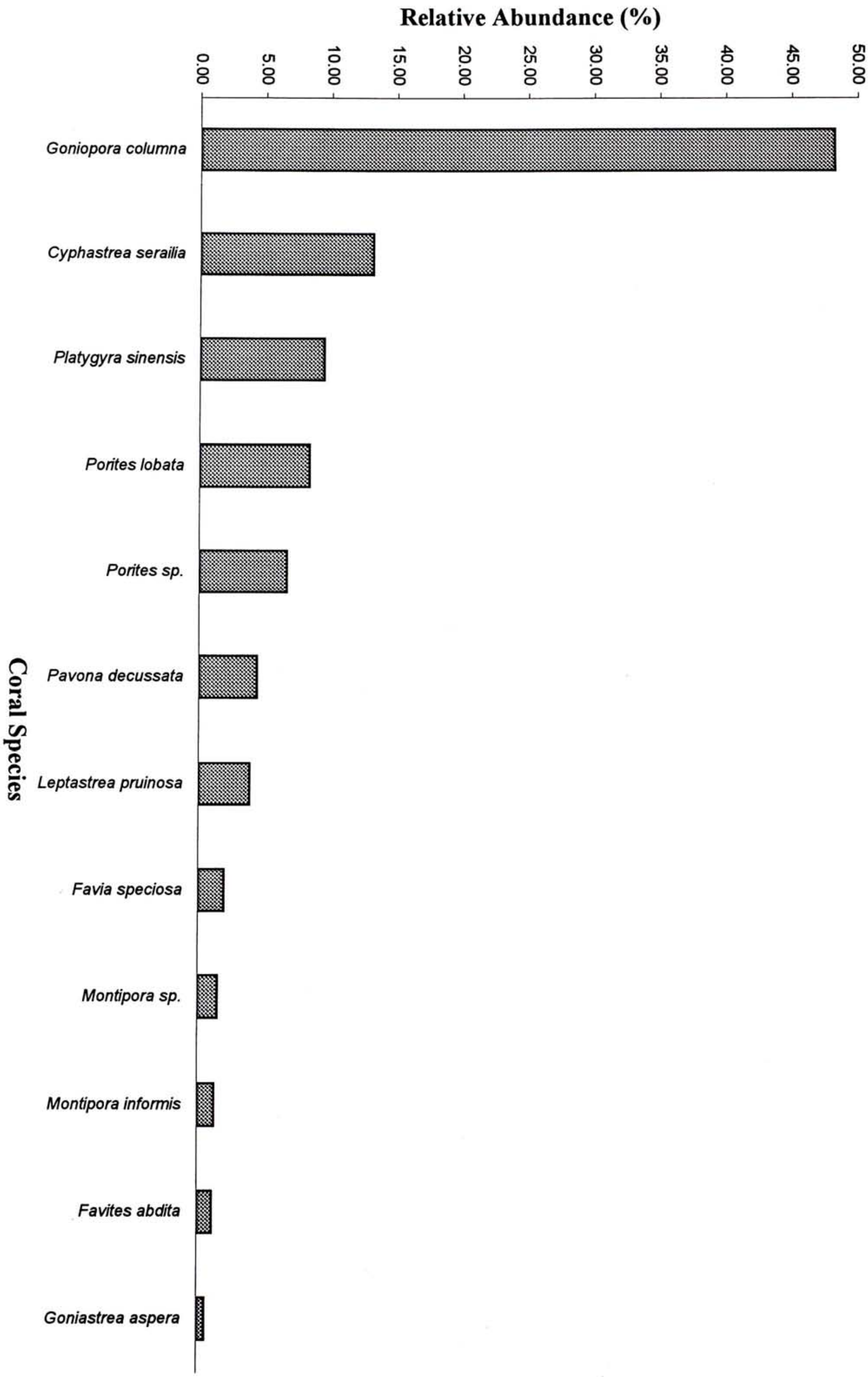
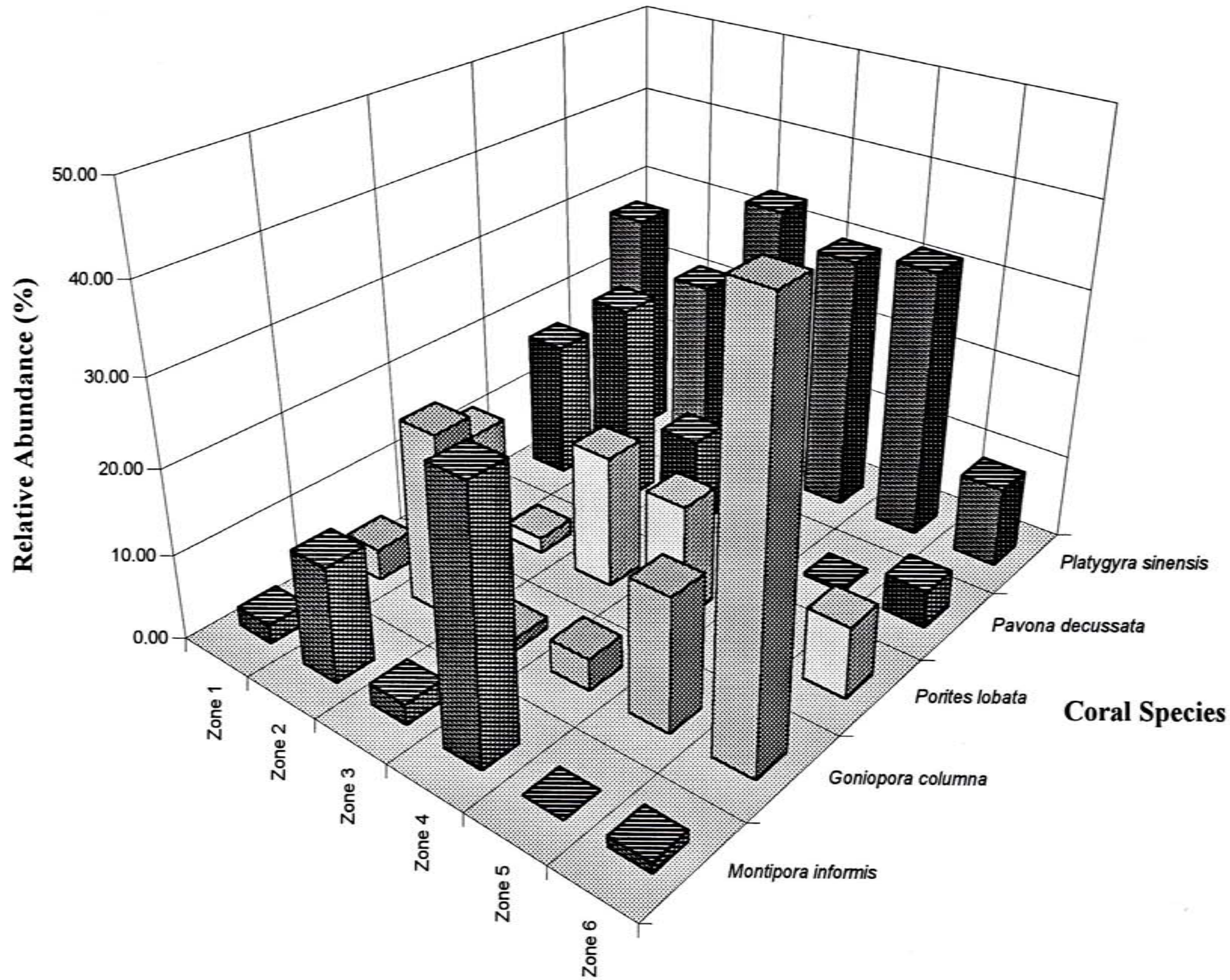

Relative Abundance (%)
0.00
5.00
10.00
15.00
20.00
25.00
30.00
35.00
Coral Species
Platygyra sinensis
Goniopora columna
Porites lobata
Cyphastrea serailia
Favites abdita
Leptastrea pruinosa
Favia speciosa
Favites pentagona
Leptastrea purpurea
Lithophyllon cf. edwardsi
Turbinaria peltata
Pavona decussata

Figure 2.11. Relative abundance of coral species found in Zone 6 (right deep sandy zone) of the study area at A Ma Wan, Ping Chau.



Relative Abundance (%)
0.00
5.00
10.00
15.00
20.00
25.00
30.00
35.00
40.00
45.00
50.00
Coral Species
Goniopora columna
Cyphastrea serailia
Platygyra sinensis
Porites lobata
Porites sp.
Pavona decussata
Leptastrea pruinosa
Favia speciosa
Montipora sp.
Montipora informis
Favites abdita
Goniastrea aspera

Figure 2.12. Relative abundance of five dominant coral species found in six defined zones of the study area at A Ma Wan, Ping Chau. For detailed description of characteristics of each zone, refer to Figure 2.5.


Relative Abundance (%)
50.00
40.00
30.00
20.00
10.00
0.00
Zone 1
Zone 2
Zone 3
Zone 4
Zone 5
Zone 6
Montipora informis
Goniopora columna
Porites lobata
Pavona decussata
Platygyra sinensis
Coral Species

In order to have a clearer picture on the difference in the community structure among the six zones, a dominance-density curve was plotted to graphically present the degree of species diversity of the coral community of each zone (Figure 2.13). The dominance-density curve was constructed by first ranking the abundance (area cover) of the species in a sequence from 1 to s, where s is the total number of species being considered. The most abundant species is assigned rank 1, the second most abundant is given rank 2 and so on, with the least abundant one receiving rank s. The abundance of each species was then plotted on a logarithmic scale against the corresponding rank. A community with a high degree of diversity will tend to have more species and more even abundance among the species, hence a more gentle slope for its dominance-density curve will be obtained. However, if the community has low species diversity, a steep curve will be resulted.

Different degrees of species diversity were observed among the six zones (Figure 2.13 and Table 2.3). Zones 1 (left shallow rocky zone) and 2 (left deep sandy zone) had the most gentle dominance-density curve, suggesting that these two zones had a high degree of species diversity. The curve for Zone 3 (middle shallow sandy zone) was the steepest, indicating that it had the lowest species diversity.

The lowest coral species diversity found in Zone 3 may be explained partly by the difference in its bottom substratum when compared with other shallow zones (Zones 1 and 5). The substratum of Zones 1 and 5 were mainly rocky while that of Zone 3 was mainly sandy. The substratum of Zones 2, 4 and 6, the deeper water zones, was also sandy, however, these zones may be subjected to lesser degree of disturbance from waves. Thus, in Zone 3, absence of a stable substratum may limit the number of corals that could settle, and those corals that already settled in this zone may easily be overturned by waves and get killed by suffocation.

Figure 2.13. Dominance-density curve of the scleractinian coral community found in six defined zones of the study area at A Ma Wan, Ping Chau. For detailed description of characteristics of each zone, refer to Figure 2.5.

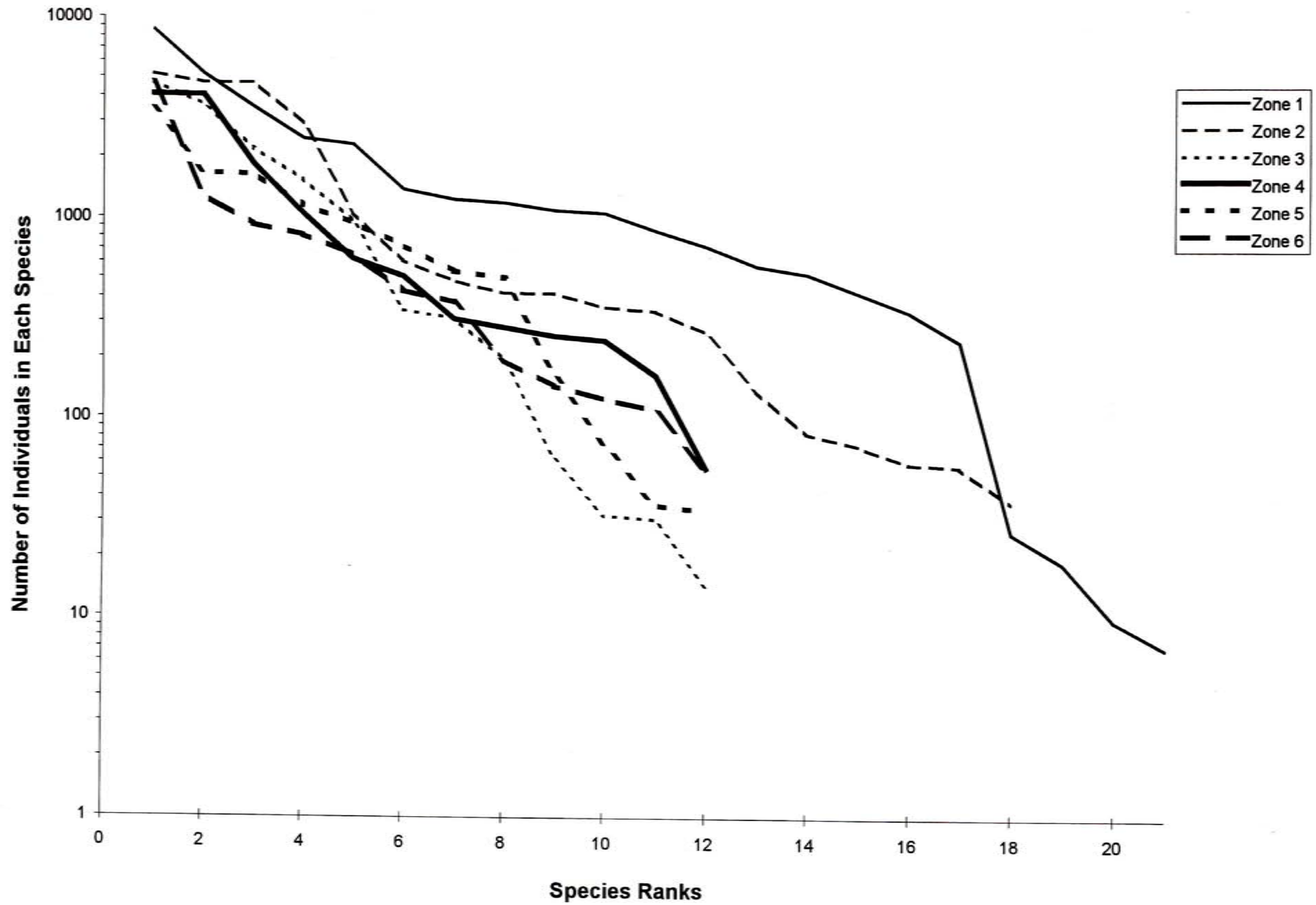

Number of Individuals in Each Species
10000
1000
100
10
1
0
2
4
6
8
10
12
14
16
18
20
Species Ranks
Zone 1
Zone 2
Zone 3
Zone 4
Zone 5
Zone 6

Table 2.3. The slope of the dominance-density curve of the scleractinian coral community found in the six defined zones described in Figure 2.5.

Zone Number	Zone Description	Slope
1	Left shallow rocky zone	-0.1303
2	Left deep sandy zone	-0.1282
3	Middle shallow sandy zone	-0.2386
4	Middle deep sandy zone	-0.1533
5	Right shallow rocky zone	-0.1809
6	Right deep sandy zone	-0.1490

In addition to the dominance-density curve, a nonparametric Kruskal-Wallis analysis of variance, with Tukey-type multiple comparisons (Zar, 1996) was also performed to test for significant difference in species diversity among the six zones. Brillouin Index calculated for each quadrat was used in the statistical test since the coral community surveyed in each zone were sampled in a non-random, systematic way (Brower, *et al.*, 1989). Zones 1 and 5 were found to have the highest mean Brillouin Index of species diversity, while Zone 3 had the lowest index value (Table 2.2). Although the zone with the highest species diversity (Zone 5) obtained by calculation of Brillouin Index was different from that obtained by dominance-density curve (Zone 1), the zone with the lowest species diversity was the same in these two calculations. However, the results of statistical test showed that the Brillouin Index of species diversity was not significantly different among different zones (Kruskal-Wallis analysis of variance, with Tukey-type multiple comparisons, total DF = 78, groups DF = 5, error DF = 74, $P > 0.05$).

While the Brillouin Index may not be different among the zones, their species composition may be different. The similarity of species composition and abundance (area cover) among the six zones was assessed by agglomerative hierarchical method of Cluster Analysis (Digby and Kempton, 1987). Inter-zone Euclidean distance and Proportional Similarity were used to produce a dendrogram and shade diagram respectively to well illustrate the results of the hierarchical method. Area cover of each coral species and its log transformation (i.e., ln (area cover +1)), which was used to reduce large aberrant values, were used to calculate the inter-zone Euclidean distance. Proportional Similarity (Brower *et al.*, 1989) between each zone was calculated by the following equation:

$$\text{Proportional Similarity, } PS = 1 - (\Sigma\,|p_i - q_i|) / 2$$

where p_i is the proportional composition of species i in the first community and q_i is the proportion of that species in the second community. A high PS value indicates a greater similarity in the community structure between the two zones.

A clear pattern of coral zonation was observed by assessing the inter-zone Euclidean distance and the inter-zone *PS* value (Figures 2.14 - 2.16). The dendrogram obtained by calculating the Euclidean distance, with either original coral area cover or log-transformed data, showed that all zones were at least 40% dissimilar from each other. Zone 1 (left shallow rocky zone) and Zone 2 (left deep sandy zone) were a pair of the most dissimilar zones found in the study area. The shade diagram, whose value was calculated by the *PS* value, also indicated that no pair of zones was over 70% similar in this community structure. Zone 6 (right deep sandy zone) was found to be the most dissimilar zone in the study area from the shade diagram displayed.

The community structure of the six defined zones was found to be significantly different from each other. The coral zonation observed might be a result of the exposure to different types and degrees of disturbance explained by each zone and the different biological responses of corals to such disturbance. However, biological interactions (e.g., grazing effects from sea urchins, competition from seaweeds) may also contribute to the zonation pattern observed in the coral community studied. Further survey should be made on the spatial distribution and abundance of other benthic organisms in the study area. In addition, further experiment could be conducted to quantify the degree of siltation disturbance and wave stress in the study area in order to verify the mechanisms responsible for the coral zonation identified in this present study.

Figure 2.14. A dendrogram for six defined zones of the study area at A Ma Wan, Ping Chau, derived by simple linkage method (nearest neighbour). The Euclidean distance calculated was based on the area cover of the coral species found within each zone. Longer Euclidean distance indicated more dissimilarity in the coral community structure. For a description of the characteristics of the different zones, refer to Figure 2.5.

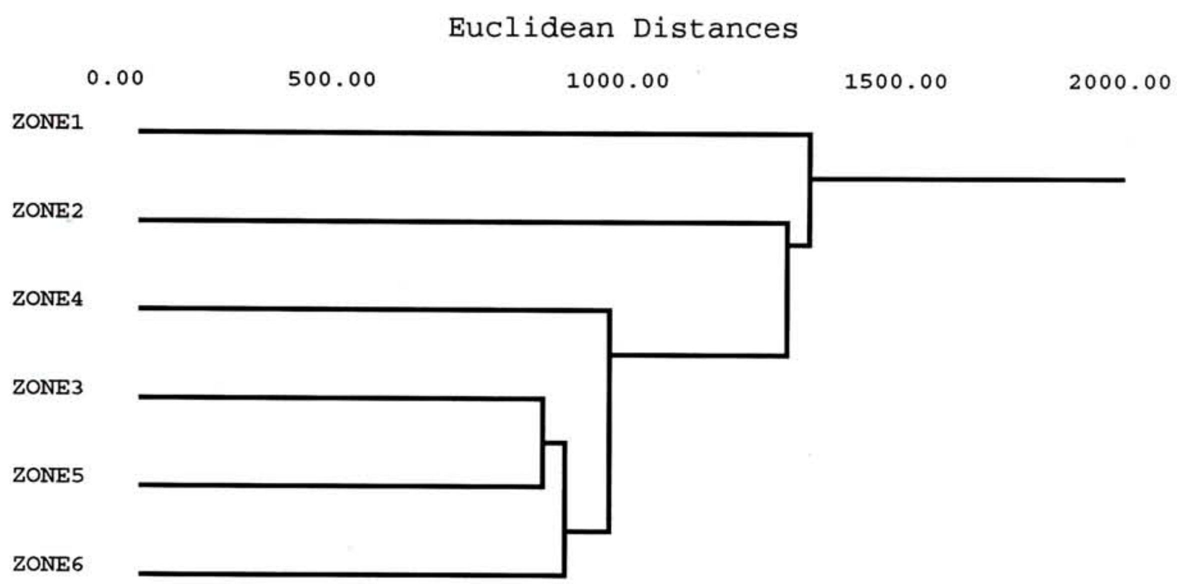

Euclidean Distances
0.00
500.00
1000.00
1500.00
2000.00
ZONE1
ZONE2
ZONE4
ZONE3
ZONE5
ZONE6

Figure 2.15. A dendrogram for six defined zones of the study area at A Ma Wan, Ping Chau, derived by simple linkage method (nearest neighbour). The Euclidean distance calculated was based on the log-transformation of the area cover of the coral species (ln (area cover + 1)) found within each zone. Longer Euclidean distance indicated more dissimilarity in the coral community structure. For a description of the characteristics of the different zones, refer to Figure 2.5.

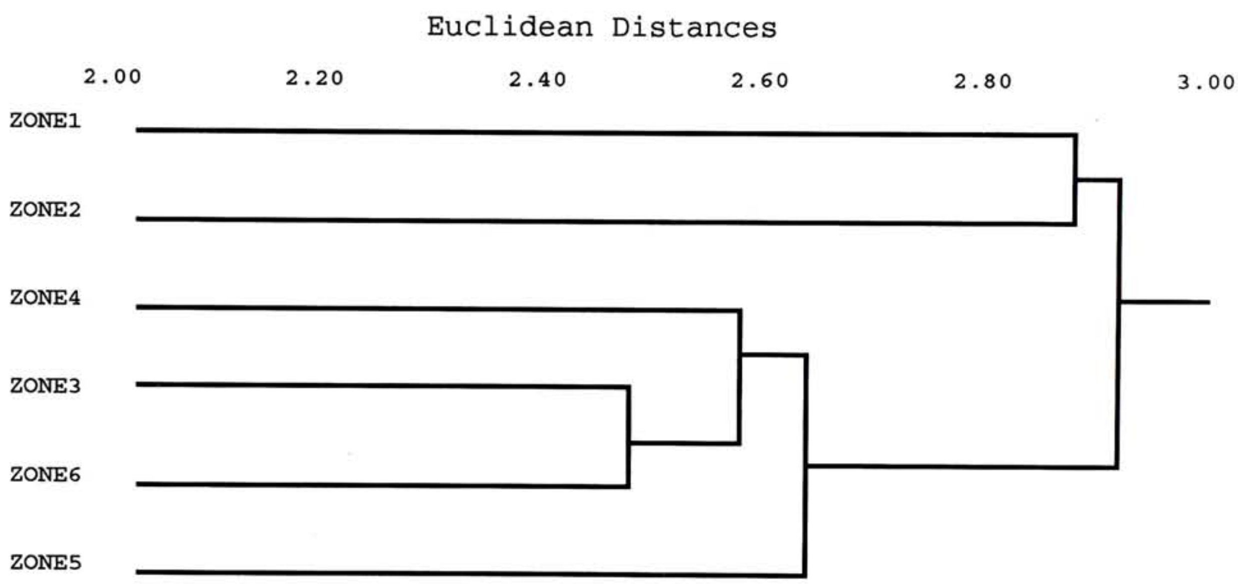
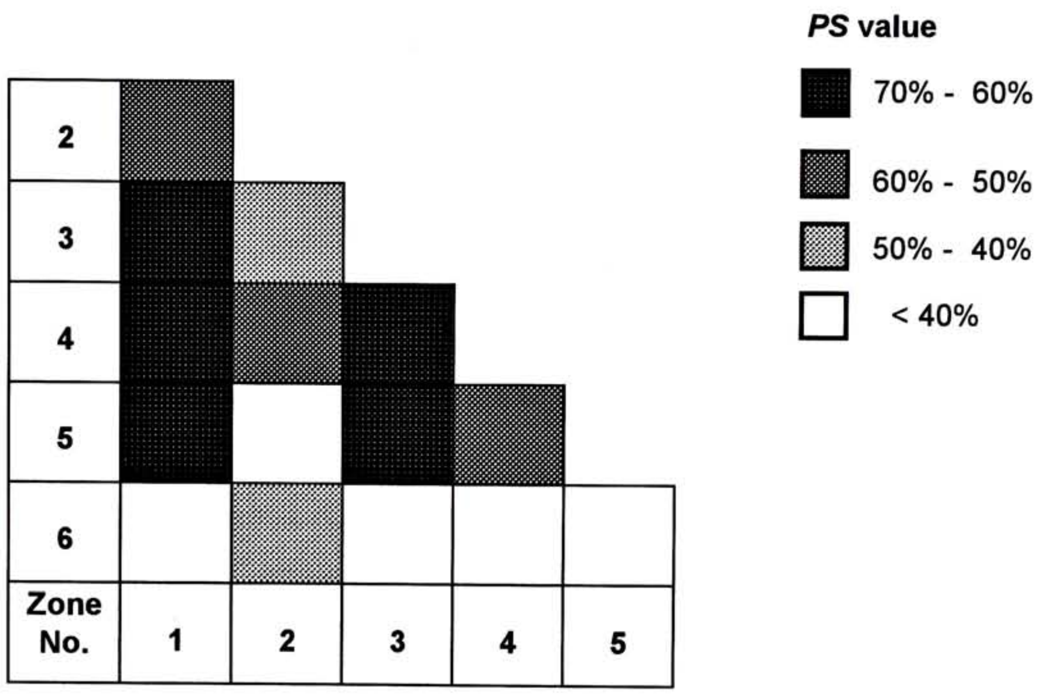

Euclidean Distances
2.00
2.20
2.40
2.60
2.80
3.00
ZONE1
ZONE2
ZONE4
ZONE3
ZONE6
ZONE5

Figure 2.16. Shaded similarity matrix diagram for six defined zones of the study area at A Ma Wan, Ping Chau. The percentage of community similarity was indicated by the proportional similarity (*PS* value) of the coral community between zones. For a description of the characteristics of the different zones, refer to Figure 2.5.


PS value
70% - 60%
60% - 50%
50% - 40%
< 40%
2
3
4
5
6
Zone No.
1
2
3
4
5

CHAPTER 3 OBJECT-ORIENTED SIMULATION OF A CORAL COMMUNITY

3.1 Introduction

Scleractinian coral community is one of the complex communities that exhibit extreme variation in community structure and diversity (Connell, 1973; Sorokin, 1993). However, mechanisms governing the stability of this community are still not completely known. Developing an ecological model to understand the behaviour of a complex system may provide one of the useful ways to study the critical point of stability and the dynamics of these sophisticated systems. In Hong Kong, the degradation of marine and coastal environment can be observed everywhere. Large area of land reclamation has already damaged lots of coastal marine communities since late 70s. A significant decrease in coral diversity and coral cover has already been observed along the Tolo Channel in north-eastern Hong Kong within a 15-year period (Scott and Cope, 1988; Cheung, unpublished data). Therefore, developing an ecological model to understand mechanisms governing the dynamical behaviour of a coral community may become an urgent need to help protect and conserve these delicate marine communities.

However, assumption of most classical models violated two basic tenets of biology (Section 1.3). The "individuality" of each organism is averaged out by a single variable or average property. In addition, most simulations do not consider organisms' local interaction. They have no real spatial representation and do not model spatial variability.

In order to address the violation of these two basic biological tenets in most of the ecological models, the idea of an individual-based approach was introduced in ecological modelling (Section 1.3). In the present research, such individual-based approach was applied in the computer simulations of a coral community using object-oriented progamming (OOP).

This Chapter presented the ecological model developed to investigate the mechanisms governing the behaviour of a coral community. Five functional groups of corals, based on their specific growth form and biological characteristics, were used in the simulation. These five functional groups resemble the five dominant coral groups identified in the preliminary field study (Section 2.4.1) in their asexual growing behaviour, competitive mechanisms with other corals and sensitivity towards changes in the environmental conditions. The results generated from the model were compared with the actual field data.

In the present model, each coral was modelled as an independent computer programme. The behaviour of each coral, including its interaction with each other, was specified within the entity itself. A reef environment was provided for the corals to interact with each other and with their local environment. There was no overall controlling programme or agent in the model. Overall behaviour of the simulated coral community emerged from local interactions among independent corals.

Effects of two physical factors were investigated in the present model. Firstly, temperature fluctuation was set to resemble the real situation in the study area. The average winter sea surface temperature (16.78 ^{0}C from January to February) found in Hong Kong was known to be lethal to corals (Kinsman, 1964) and should be important in structuring the natural coral community. Secondly, as the coral community studied in the field was a shallow water coral community (Section 2.2) known to be sensitive to wave stress and storm disturbance (Porter *et al.*, 1981; Woodley *et al.* 1981), storm disturbance was considered as a physical disturbance in the model. Different degrees of disturbance were set in the simulation so as to reveal the response of a coral community towards this type of physical disturbance.

3.2 Object-oriented Programming (OOP)

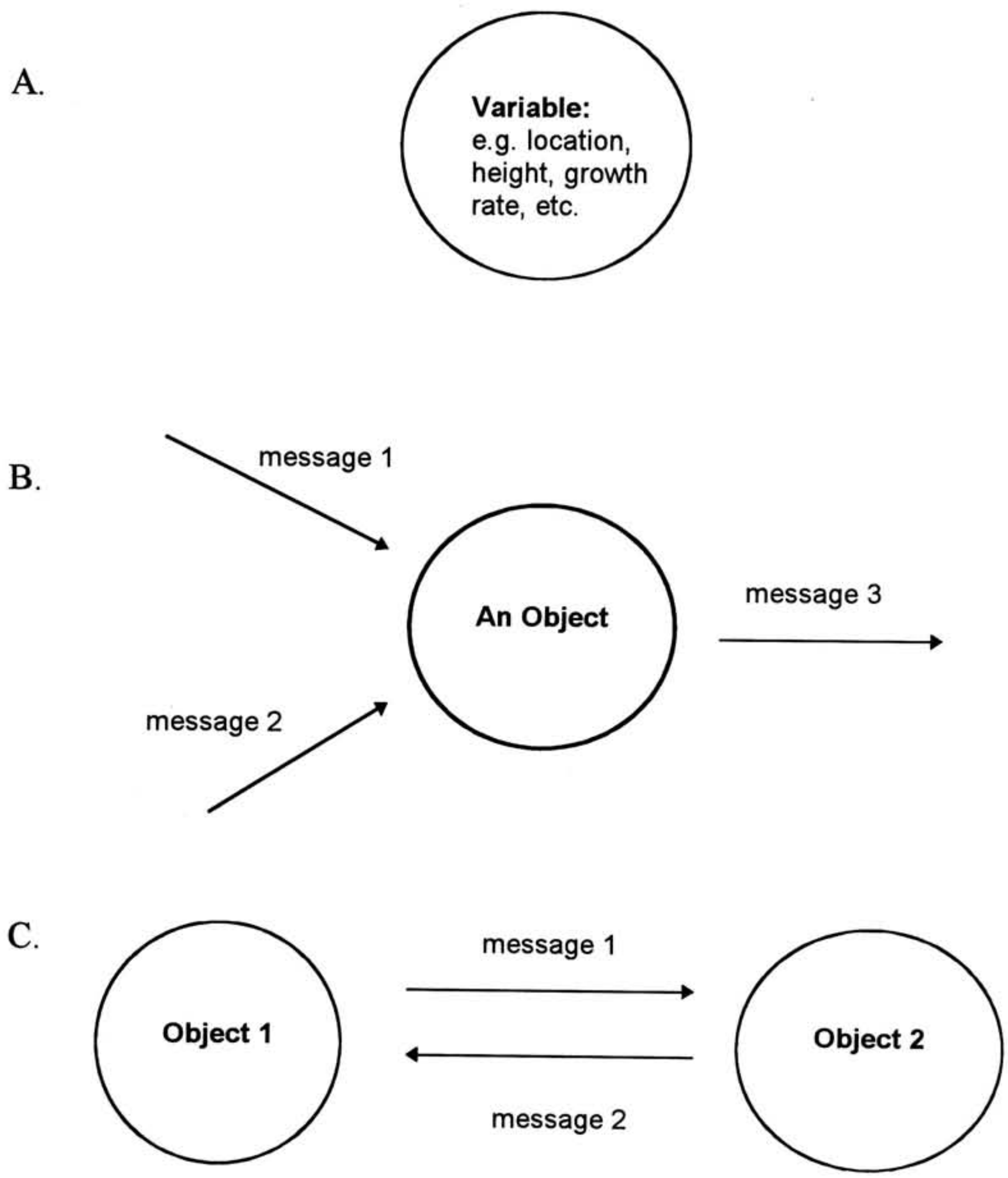
The model was written in an object-oriented programming language. Smalltalk/V (ParcPlace Systems, Inc., U.S.A.) is a convenient language to create computer representations of individual actors in a complex system. The software used for the model is Visual Smalltalk Enterprise (ParcPlace-Digitalk, Inc., U.S.A.), which has a programming environment for describing objects and the interactions between them. As understanding the object structure of the model is essential to understanding the significance of this computer experiment, object-oriented programme is reviewed briefly here.

3.2.1 Objects

The most fundamental concept of object-oriented programming is "Object". An "Object" can be anything - it can be a tree, a square, a chair, etc. Each object will have its own variables, and each variable may be represented by a range of characteristics. For example, a specific tree (object) will have a specific height and biomass (variables), which may change over time (hence represented by a range of numbers or characteristics). Each object also has its own method to interact with other objects. When an object receives a message, it will perform a task, or may act on other objects. An object can receive messages from, or send messages to other objects. Each object can also respond to any events occurring in the programming environment (Figure 3.1).

Figure 3.1. The properties of an object in object-oriented programming. A. An object can have its own variables, B. receive or send messages, C. respond to a message sent from another object.

An Object


A.
Variable:
e.g. location,
height, growth
rate, etc.
B.
message 1
An Object
message 3
message 2
C.
Object 1
message 1
message 2
Object 2

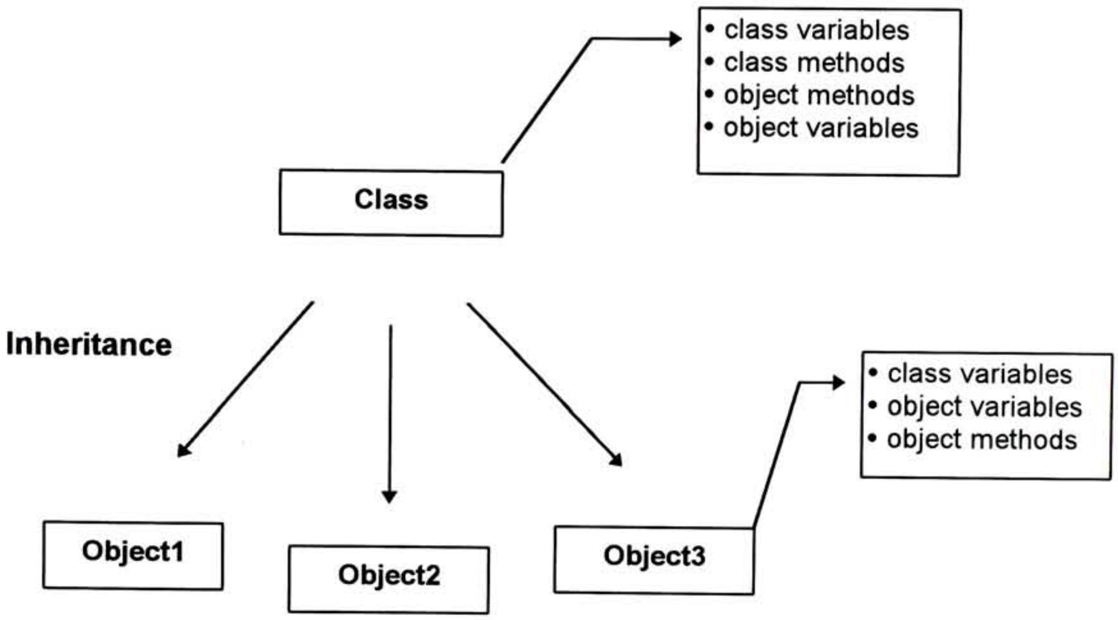
3.2.2 Classes, Hierarchies and Inheritance

Many similar objects (instances) will make up a specific class. For example, the object, **aTree**, would be an object classified in a class called **Tree**. This is similar to the ecological concept of many similar (but not identical) individuals making up a population. Each object will have its own variables and methods to act in the simulating environment, and its variables and methods are inherited from which class it belongs to. All classes are organized into hierarchies. Each class can have its subclass, just like in a family tree which represents the ancestor / descendent relationships among a set of classes. Subclass can inherit the variables and methods declared from its parent class. (Figure 3.2).

3.2.3 Object-oriented Simulation

Writing an object-oriented simulation involves constructing class to represent each type of objects in the simulation, creating specific objects with appropriate state variables, and allowing them to interact by sending messages or triggering events to each other. As objects in the computer model and organisms in nature are in one-to-one correspondence, messages sent among objects in the computer model thus represent the interactions among organisms. A life-like behaviour can then be studied in this "artificial ecosystem", in which the overall behaviour of a system is generated from local interactions between each independent object in the computer environment.

Figure 3.2. Hierarchical structure of class and objects in object-oriented programming.


• class variables
• class methods
• object methods
• object variables
Class
Inheritance
• class variables
• object variables
• object methods
Object1
Object2
Object3

3.3 Object-oriented Simulation of a Five-Coral Community

In the simulation of the dynamical behaviour of a coral community, **BenthicEnvir** and **Coral** were defined for the class of reef environment and coral respectively. The corals, or coral colonies (**Coral** objects), were allowed to grow and interact in a reef environment (a **BenthicEnvir** object) (Figure 3.3). Changes in the spatial distribution and area cover of each coral were followed during model operation. Each coral inherited the same attributes (variables) from class **Coral** but had different values and charateristics in the variables, and thus behaved differently in the reef environment according to its own specific characteristics.

3.3.1 Class BenthicEnvir

An object (instance) of class **BenthicEnvir** represents a reef environment for the corals to grow. Area of a reef environment can be set according to one's interest by specifying the length (**spaceLength**) and width (**spaceWidth**) of a reef environment, and is calculated by the following equation:

Area of a reef environment = its length (**spaceLength**) x its width (**spaceWidth**)

The reef environment will contain a number of unit areas (pixel). Each unit area represents a location for the coral polyps of each coral to grow. The number of unit area for the corals to grow is equal to the total area of the reef environment.

The reef environment (**BenthicEnvir** object) will contain the information of all physical conditions and status of all corals inside (Figure 3.3). Different physical conditions can be set at different time in the simulation according to one's interests. Three types of physical conditions can be varied in the reef environment. They are sea temperature (**seaTemp**), sea level (**seaLevel**) and disturbance level (**stormLevel**). Sea temperature and sea level were chosen as variables because they were critical to the growth and survival of corals (e.g. Kinsman, 1964; Jokiel and Coles, 1974; Baker and

Weber, 1975). In addition, among different types of physical condition which are important to coral growth (e.g. salinity, light intensity), only sea temperature and sea level had actual monthly variation record in Hong Kong. Therefore only sea temperature and sea level could be simulated to resemble the actual physical environment of the coral community found in A Ma Wan, Ping Chau. Furthermore, as physical disturbance (hurricane) was one of the important factors in structuring coral community (e.g. Woodley *et al.*, 1981; Dollar and Tribble, 1993; Andres and Witman, 1995), its effects on the dynamical structure of a coral community were thus considered for investigation. The value of disturbance level in the simulation is given as the percentage of area in the reef environment that will be disturbed in each disturbance event. The percentage of area that will be disturbed is thus calculated by the equation below:

$$\boxed{\text{Percentage of area disturbed} = (\text{disturbance level}) \times (\text{area of reef environment}) \div 100}$$

The location in the reef environment being disturbed is randomly chosen during disturbance. When a location in the reef environment is disturbed, coral polyps at that location will have a chance to be removed or killed. If a coral polyp is removed by disturbance, it will disappear from the reef environment, while if it is killed, it will only become a dead coral polyp. The chance of a coral polyp being killed or removed in the disturbance will depend on the sensitivity and response assigned to it at the beginning of the simulation.

3.3.2 Class Coral

Class **Coral** includes variables which represent the biological characteristics of a coral. The growth form of a coral, or a coral colony (**Coral** object) was defined by its species number (**speciesNum**). The species number of a coral will also indicate its competitive mechanism and sensitivity towards environmental changes. The information of a coral's polyps will be represented by the other variables, which indicate their location, height, living status (whether it is alive, dead or being overtopped by other coral polyp), growing activities and interacting activities for competition. Each coral will have its own linear growth rate (**growthRateLinear**) for its polyps to grow up, and radial growth rate (**growthRateRadial**) for its polyps to reproduce asexually and grow laterally.

Class **Coral** also includes methods to represent the growing behaviour of a coral, or a coral colony (**Coral** object). The coral will let its polyps grow up according to its linear growth rate (**growthRateLinear**) when it receives the message **GrowingUp**. The polyps of a coral will also reproduce asexually according to its radial growth rate (**growingRateRadial**) when it receives the message **GrowingRadial** (Figure 3.3). For simplification, only those polyps along the margin of a coral colony are considered as the "growing polyps" and will reproduce asexually.

The growth rate (linear or radial growth rate) of each coral polyp will be varied in a positive sin-function distribution (Figure 3.4), so as to allow the development of individual variation in the model. Everytime when a coral polyp grows, its growth rate is randomly assigned from a range of growth rate values distributed in a sin-function curve, with the amplitude of the curve being equal to the value of corresponding growth rate variables (**growthRateLinear** and **growthRateRadial**). The chance of a growth rate value that is assigned to a coral polyp will be equal to the frequency of this growth rate value appearing in the sin-function curve. The sin-function distribution used in the present model is also a simplification to allow individual variations.

However, if the coral is sensitive to sea temperature in the simulation, the actual growth rate (linear or radial growth rate) of its polyps will then be affected by the sea temperature. When the sea temperature is below the general optimal temperature for coral growth, the growth rate of its polyps will be re-calculated by the following equation:

Actual growth rate = original growth rate x (present sea temperature - temperature limit of the coral) ÷ (general optimal temperature for coral growth- temperature limit of the coral)

Such linear proportional effect of the temperature set on the growth rate of a temperature-sensitive coral is a linear simplification of the curvilinear relationship between coral growth and temperature found by Jokiel and Coles (1977). The general optimal temperature for coral growth was set to be $25^{0}C$, which falls within the temperature range for the best coral growth in nature (Kinsman, 1964).

Each coral, or each coral colony (**Coral** object) will reproduce sexually when receiving the message **spawnLarvaeNum**. A coral will be "informed" of the number of larvae that it will spawn when it receives the message. The spawned larvae will go randomly to any locations within the reef environment. Successful settlement of coral larvae will only occur when the location where the larvae will go is free of any other coral polyps, or have dead coral polyps only. The successfully settled coral larva will become the centre of a new coral colony and will start to grow when it receives the growing messages (**GrowingUp** and/or **GrowingRadial**).

Each coral, or each coral colony (**Coral** object) will interact with each other according to its own competitive mechanism assigned. Interaction will occur when the coral receives the messages **Interacting** or **Revenging**. **Interacting** message causes the coral's "growing polyps" (those polyps at the margin of a coral colony) to compete with other coral's polyps for a space to grow. **Revenging** message triggers the coral's polyps, which are also situated at the margin of the coral colony, to perform revenging aggressive activities towards other coral's polyps. The number of coral polyps responding to the **Revenging** message and the effective range of aggressive activities will depend on the coral's competitive mechanism.

Figure 3.3. A general picture on the interaction between each coral (a **Coral** object), and the relationship between the corals and a reef environment (a **BenthicEnvir** object).

A Reef Environment (a **BenthicEnvir** object)

- lists out the temperature, sea level, disturbance level, area of the reef environment, space availability, occupied space and information of each coral.

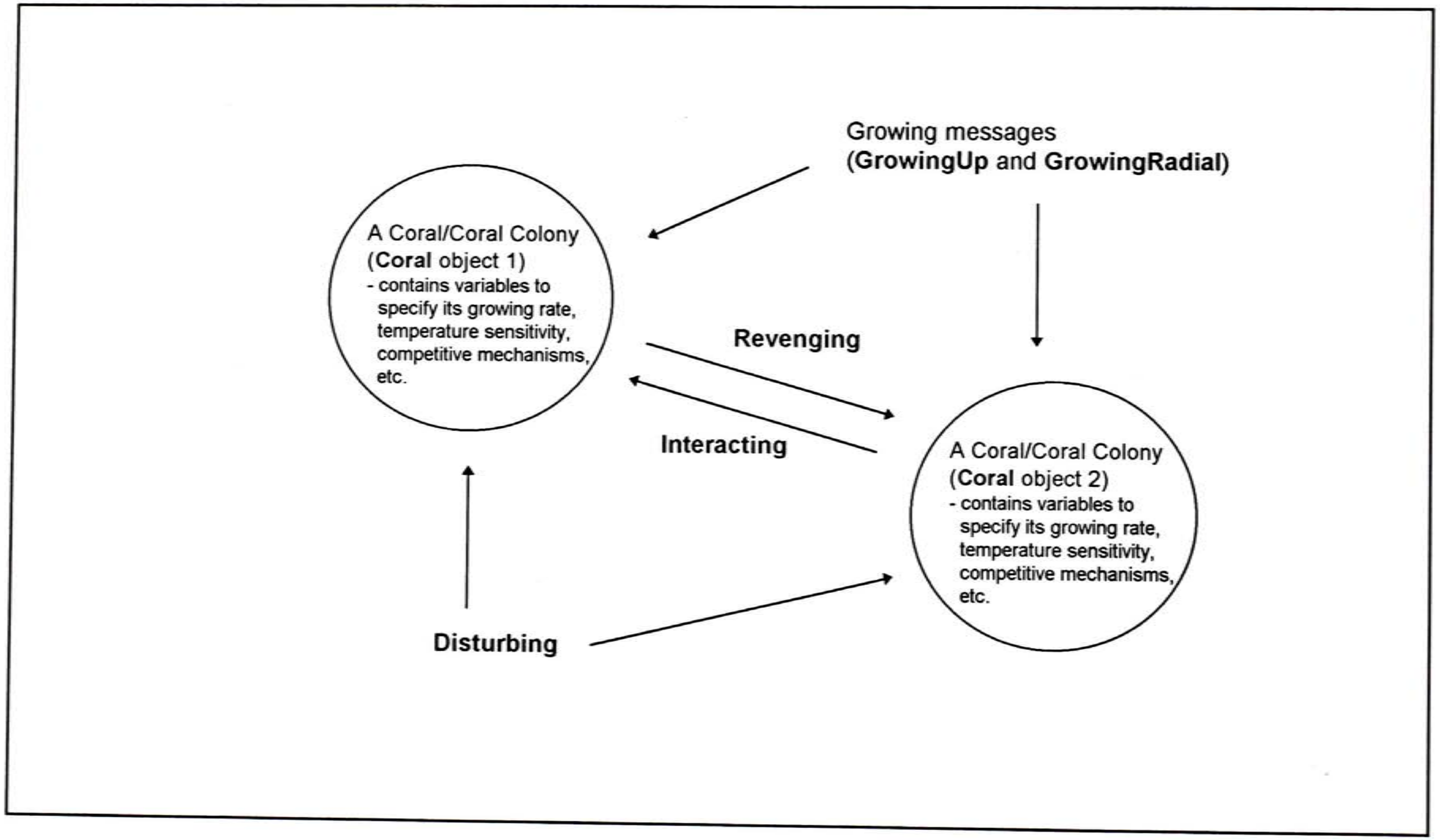
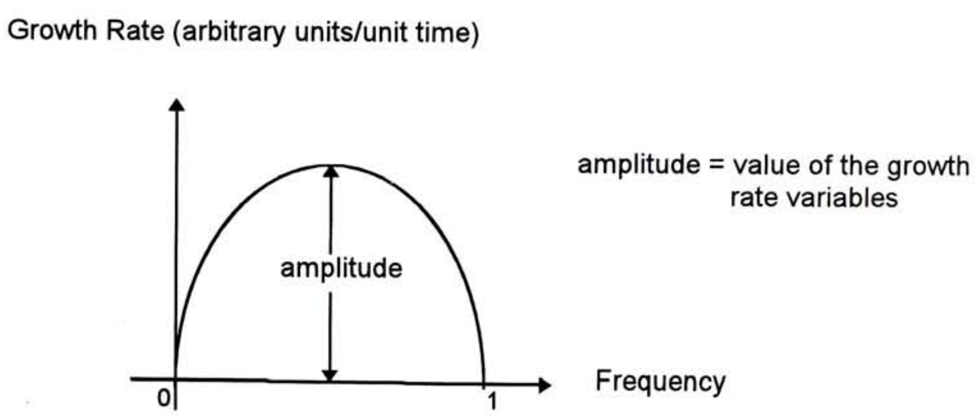


Figure 3.4. The distribution of growth rate of the polyps of a coral (**Coral** object).


Growth Rate (arbitrary units/unit time)
amplitude
amplitude = value of the growth rate variables
0
1
Frequency

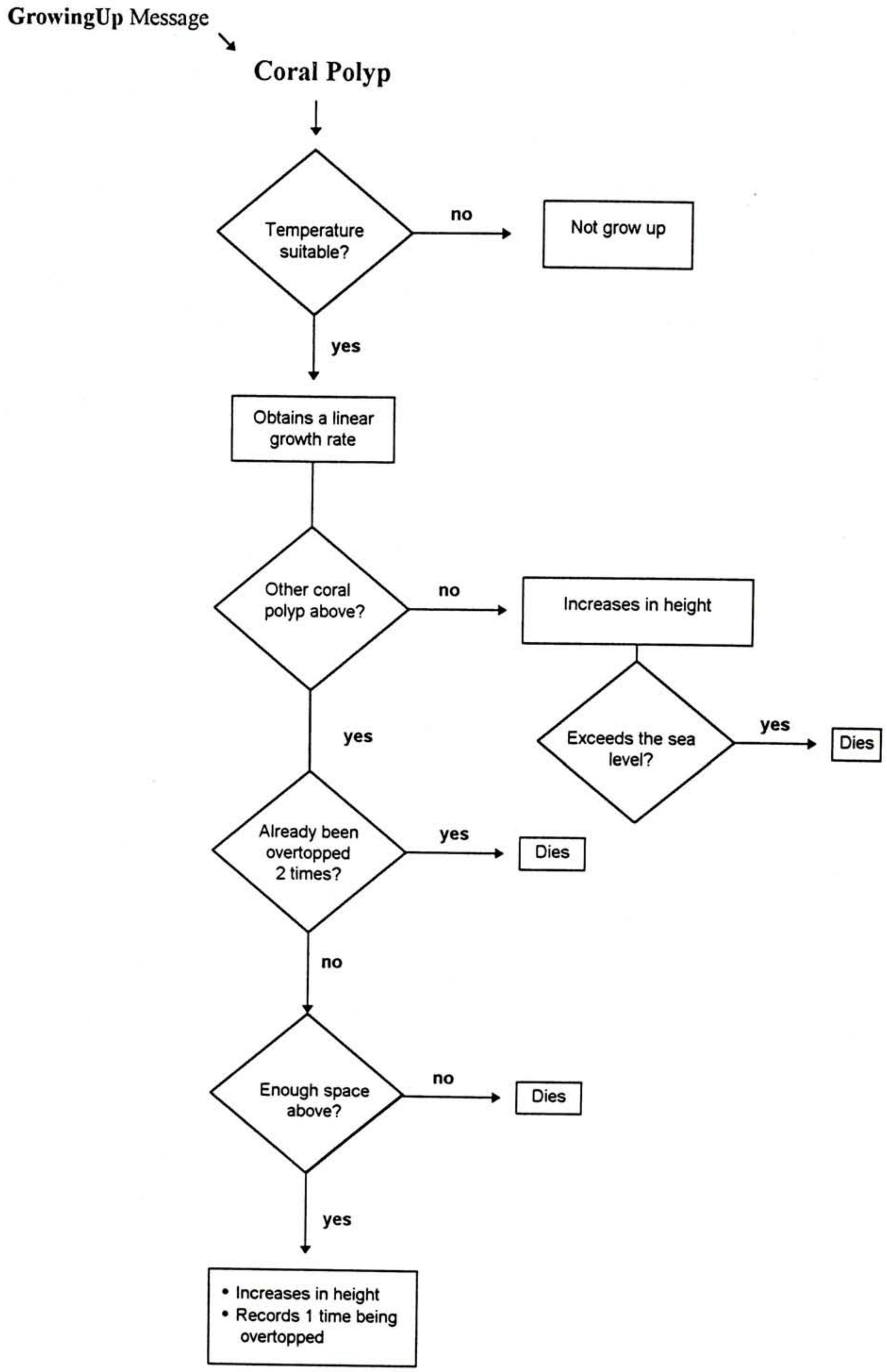
3.3.3 The Objects Behaviour

Each coral, or each coral colony (**Coral** object) will perform growing-up, growing-radial (asexual reproduction), spawning (sexual reproduction) and interactions with other coral when it receives the acting message during simulation. All types of the behaviour of a coral were chosen by if-then rules.

When a coral, or a coral colony (**Coral** object) receives the growing message, either **GrowingUp** or **GrowingRadial**, it will detect first whether the sea temperature of the reef environment (a **BenthicEnvir** object) is suitable for growing or not. If the sea temperature is below its temperature limit for growth, then the coral polyp will not grow. If the temperature is suitable, each coral polyp will grow according to its randomly assigned growth rate (Section 3.3.2).

During growing-up, each coral polyp will detect whether there is other coral polyp situated above it. If there is none, the coral polyp will grow up to a new height. However, if the new height of a coral polyp exceeds the sea level of the reef environment, then the coral polyp will die immediately. If there is another coral polyp situated above it, then the coral polyp will check whether it itself has already been overtopped two times in the past. If it is so, then the coral polyp will die and become a dead coral polyp. Otherwise, the coral polyp will detect whether there is enough space above it for it to grow up. If there is enough space, the coral polyp will grow up to a new height and recording itself as being one time, or one more time overtopped by other coral polyp (if the coral polyp has already being overtopped). If there is not enough space instead, the coral polyp will die (Figure 3.5).

Figure 3.5. Flow chart of the growing-up method for each coral polyp when a coral (**Coral** object) receives the **GrowingUp** message.


GrowingUp Message
Coral Polyp
Temperature suitable?
no
Not grow up
yes
Obtains a linear growth rate
Other coral polyp above?
no
Increases in height
Exceeds the sea level?
yes
Dies
yes
Already been overtopped 2 times?
yes
Dies
no
Enough space above?
no
Dies
yes
• Increases in height
• Records 1 time being overtopped

When a coral is triggered to reproduce asexually, only those polyps along the margin of the coral colony are considered as the "growing polyps" and will reproduce by way of binary fission. Reproduction will start from the oldest "growing polyps" to the youngest "growing polyps". Each "growing polyp" will detect first whether there is any free space around it. It will detect the space in eight directions - north, north-east, east, south-east, south, south-west, west and north-west direction. If there is free space around, the "growing polyp" will reproduce in a random direction. However, if all space around is occupied, then the "growing polyp" will compete (**Interacting**) with the surrounding coral polyps (Figure 3.6).

Types of interaction decided for each coral represent the general coral competitive mechanisms reviewed by Lang and Chornesky (1990). Five types of mechanism were considered and were used in the simulation. They were overgrowing, overtopping, histoincompatibility, and direct killing by sweeper tentacles or sweeper polyps, which are different competitive mechanisms used by the five dominant coral groups identified in the coral community of Ping Chau (Section 2.4.1).

Direct killing may result from all types of competitive mechanism except overtopping. Overgrowing behaviour will let "growing polyp" reproduce a new coral polyp on other coral polyp. The covered polyp will be killed in this type of interaction.. Histoincompatibility, direct killing by sweeper tentacles or sweeper polyps, will cause a direct killing of the other coral polyps within the effective range defined by the acting polyp. However, the acting polyp will not grow on the killed polyps in these three types of interaction.

Indirect killing will result from the overtopping competitive mechanism. In this type of competitive mechanism, the "growing polyp" will grow above other coral polyp and leave a space in between. The polyps being overtopped will continue to have all the growing and interacting activities. However, they will die later if they are overtopped continually for two time intervals by the coral polyps above them (Figure 3.5).

Results of the competition **(Interacting)** will allow those "growing polyps" with overgrowing or overtopping competitive mechanism to know which direction(s) it can win in the competition. If there are several directions of the occupied spaces that can be won, the "growing polyp" will just randomly choose a direction to reproduce a new polyp, with a preference to those occupied by the dead coral polyp. Depending on the competitive mechanism used by the "growing polyp", the newly-formed polyp may then kill the coral polyp that lost in the competition.

The polyp lost in the competition may trigger itself (if it is not killed) or its adjacent partners to become a "revenging polyp" to perform aggressive revenging activities. Such triggering will only occur for those polyps at the margin of a coral colony. Whether a polyp will become a "revenging polyp" or not will depend on the competitive mechanism assigned to it.

Corals will revenge **(Revenging)** and perform aggressive killing action. During revenging, those coral polyps that have been triggered to become "revenging polyps" will perform the revenging task. Each "revenging polyp" will first detect whether all the other coral polyps are within its effective range for revenge. The effective range is determined by the extending distance, which is assigned according to the competitive mechanism of the "revenging polyp". The effective revenging range is equal to a semi-circular cylinder in front of the "revenging polyp", with the "revenging polyp" as the centre of the vertical face of this semi-circular cylinder. The height of this cylinder is equal to two times the length of the extending distance, while the radius of it is the same as the extending distance. All the detected coral polyps will be killed by the "revenging polyp" (Figure 3.7).

In fact, all the corals are generally kind and forgiving. All "revenging polyps" will restore to become normal coral polyps after the revenging activities. Coral polyps will become "revenging polyps" only when they are triggered again in the next competition.

The height of newly-formed polyps will be equal to one minus the height of the polyp that reproduces them. Such setting is just an arbitrary method to make the newly-formed polyps shorter than the old one. However, if the competitive mechanism of a coral is overtopping, the newly-formed polyp will be formed at a "starting level". The newly-formed polyps will then increase their height starting from "starting level" when they are triggered to grow up. The "starting level" of a newly-formed polyp is equal to an average value of the height and the "starting level" of the polyp reproducing itself.

Figure 3.6. Flow chart of the asexual reproduction method for a "growing polyp" when a coral (**Coral** object) receives the **GrowingRadial** message.

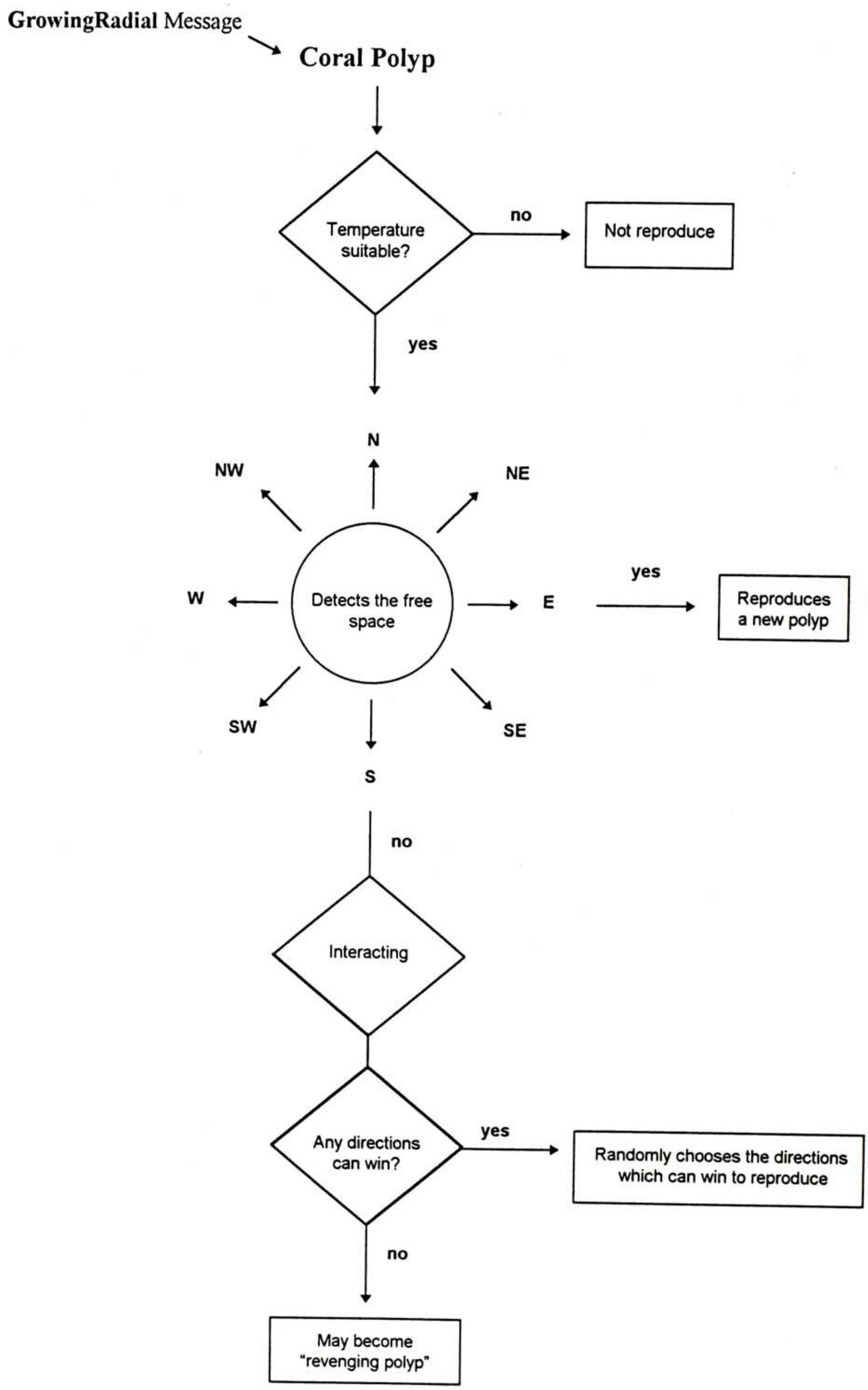
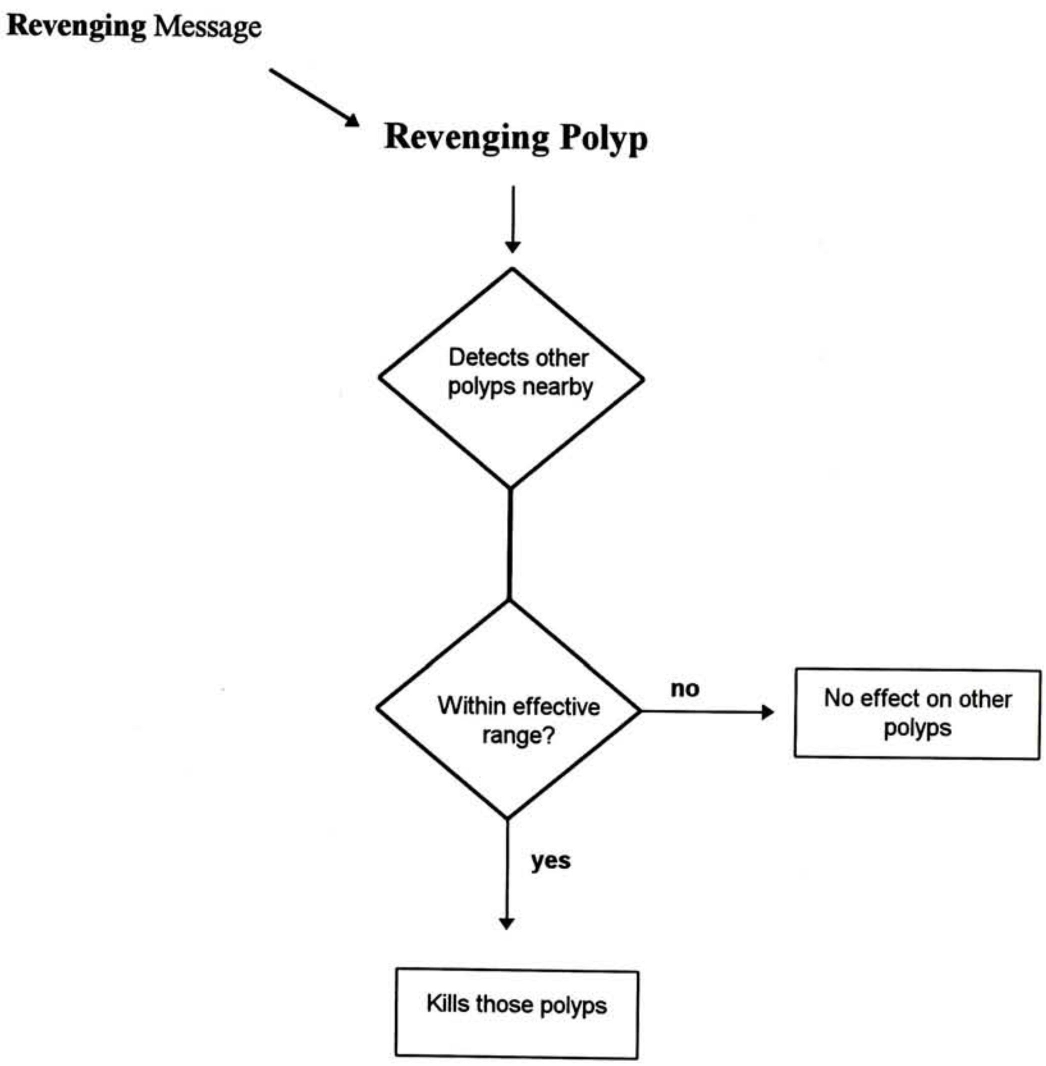

GrowingRadial Message
Coral Polyp
Temperature suitable?
no
Not reproduce
yes
N
NW
NE
W
Detects the free space
E
yes
Reproduces a new polyp
SW
SE
S
no
Interacting
Any directions can win?
yes
Randomly chooses the directions which can win to reproduce
no
May become "revenging polyp"

Figure 3.7. Flow chart of the aggressive revenging method for a "revenging polyp" when a coral (**Coral** object) receives the **Revenging** message.


Revenging Message
Revenging Polyp
Detects other polyps nearby
Within effective range?
no
No effect on other polyps
yes
Kills those polyps

3.3.4 The Simulation

Time scale in the simulation was on yearly basis. Each coral (**Coral** object) was triggered to grow, interact with other corals and respond to the changes of physical conditions of the reef environment six times in every year, i.e., the corals were triggered every two-month in the simulating environment. The simulation started with each coral group having ten larvae successfully settled in the reef environment, hence 50 corals (**Coral** objects) from five coral groups were the starting units in each simulation. Everytime when a coral was triggered, it behaved in the following sequence: growing up (**GrowingUp**) first, reproducing asexually (**GrowingRadial**) and interacting with other corals (**Interacting** and **Revenging**). One larva of each coral group was allowed to be released into the reef environment once a year (in the period of May to June). As the effects of different sexual reproductive strategies were not investigated in the present model, the setting of spawning one larva from each coral group per year was just a way to increase the chance of interaction among the corals of different coral groups in each simulation.

3.3.4.1 The Reef Environment

A size with 50x75 arbitrary units (pixels) was set as the reef environment in the simulation. The resulted number of unit area (pixel) for the corals to grow in the simulating environment was then equal to 3,750 (Section 3.3.1). Sea temperature was varied throughout the year, however, the sea level was kept at a constant in the reef environment (Table 3.1).

Variation of sea temperature used in the simulation was the same as that of average sea surface temperature recorded in Hong Kong (Wagnan Island) between the years of 1961 - 1990. The sea temperature of 17 ^{0}C was known to be a limit for coral growth, while 25 ^{0}C - 29 ^{0}C was the range for optimal growth (Kinsman, 1964). Since the effects of sea level variation were not investigated in the present model, the sea level (**seaLevel**) was arbitrarily set to provide a relatively unlimited space for the corals to grow up during the simulation.

3.3.4.2 Characteristics of the Corals in the Simulation

Each coral or each coral colony (**Coral** object) was assigned to any one of the five coral groups in the computer model. The five coral groups simulated had their own characteristics, competitive mechanisms and sensitivity towards the change in environmental conditions, and were set to resemble the five dominant groups of coral identified in the coral community of Ping Chau (Section 2.4.1). These five coral groups were massive-form or castle-like corals of Family Faviidae, foliaceous *Pavona decussata*, branching form or tabular form corals of Family Acroporidae, mushroom-like corals with elongated polyps (belong to genera *Goniopora* or *Alveopora* of Family Poritidae) and *Porites lobata* of Family Poritidae. The biological characteristics and types of behaviour of the five coral groups set in the simulation are described in Table 3.2.

The relative differences in growth rate of the five coral groups simulated in the computer model were set according to generalization of the results found by Barnes (1973), Buddemeier and Maragos (1974), Baker and Weber (1975), Gladfelter *et al.* (1978), Hubbard and Scaturo (1985), Hughes and Jackson. 1985, Guzmàn and Cortės (1989) and Sorokin (1993). In general, the growth of branching form / tabular form corals (Group 4 corals) was set at a rate faster than that of foliaceous corals (Group 2 corals), which was in turn faster than that of the massive form, castle-like and mushroom-like corals (Groups 1, 3 and 5 corals) Groups 1, 3 and 5 corals were set to have same growth rate in the simulation.

The sensitivity of corals to the variation in temperature was set according to the findings of Kinsman (1964), Jokiel and Coles (1974) and Coles and Jokiel (1978). Branching / tabular form corals (Group 4 corals) were the most temperature sensitive corals in the simulation. They had the highest temperature limit for growth than the rest of the other growth forms and their growth rate would vary proportionally with the temperature if the sea temperature was below the optimal temperature for coral growth. Foliaceous corals (Group 2 corals) were set to be the second most temperature sensitive corals with their temperature limit for growth lower than that of branching / tabular form corals (Group 4 corals). However, their growth rate would still vary proportionally with the temperature if the sea temperature was below the optimal temperature for coral growth. The rest of the coral groups were less sensitive to temperature change, and their growth rate did not vary with the sea temperature change. The temperature limit for the growth of massive form / castle-like corals (Group 3 corals) and mushroom-like corals (Group 5 corals) was the same as that of foliaceous corals (Group 2 corals), while that of massive form *Porites lobata* (Group 1 corals) was set at the lowest. Massive form *Porites lobata* (Group 1 coral) was thus simulated as the least temperature sensitive coral in the computer model.

Different responses towards disturbance were set for each coral group based on the general behaviour of that coral group observed in nature. Massive form corals were observed to have a very low chance of being overturned or dislodged in natural coral community during disturbance (Woodley *et al.*, 1981). Such response was therefore set for the massive form or castle-like corals (Coral Groups 1 and 3) in the model. The body form of the mushroom-like coral (Coral Group 5) is such that its base area is smaller than the top area, hence it is more likely to be overturned by the storm. Therefore, its chance of being overturned was set higher than that of the massive form or castle-like corals in the model. When the coral colony was overturned, it would be removed and would totally disappear from the reef environment.

Breaking of parts of the colony was observed in branching or tabular form corals during disturbance (Porter *et al.*, 1981; Woodley *et al.*, 1981; Hobson *et al.*, 1995; Lirman & Fong, 1995). Therefore, part of the colony of branching or tabular form coral (Coral Group 4) would be broken in the simulation when it was disturbed. The broken part of the colony would be removed from the reef environment. Finally, the structure of foliaceous coral (Coral Group 2) was also set to be broken and removed from the reef environment, but breaking would occur only at the points being disturbed.

3.3.4.3 Disturbance

Different sets of simulations with different levels of disturbance - low, intermediate and high (which correspond respectively to 10%, 25%, 50% of the reef environment being disturbed) were investigated to reveal the effects of disturbance on coral community. Disturbance was set to occur at one fixed time (in the period of July to August, which corresponds to the typhoon period in Hong Kong) in each year of the simulation. Another set of the simulations with disturbance occurring randomly once in each year was also examined and an intermediate disturbance level was used in this set of simulations. A set of simulations without disturbance was run as control for comparison. Each simulation was run for a period of ten years time or was ended when the reef environment was completely occupied by the corals. Twenty simulations were run for each type of disturbance, including the control.

Table 3.1. Physical conditions of the reef environment in each simulation.

Month	Jan.-Feb.	Mar.-Apr.	May-June	July-Aug.	Sept.- Oct.	Nov.-Dec.
Sea Temperature (^{0}C)	17	19	26	28	27	22
Sea Level (Arbitrary units)	500	500	500	500	500	500

Table 3.2. Biological characteristics, competitive mechanisms and sensitivity towards different physical conditions of each coral group in the simulation.

Coral Group No.	Corresponding Coral Groups in Nature	Instant Linear Growth Rate (pixels/unit time)	Instant Radial Growth Rate (pixels/unit time)	Temp. Limit for Growing (^{0}C)	Sensitivity to Temp.	Response & Sensitivity towards Disturbance	Competitive Mechanisms
1	Massive Form *Porites lobata*	1	1.5	16	No	• the polyp will become dead polyp with a chance of 10% when it is disturbed • whole colony will be overturned and removed from the reef environment by a chance of 1%	• overgrowing
2	Foliaceous *Pavona decussata*	1.5	2	18	Yes	• each polyp will be removed from the reef environment by a chance of 25% when it is disturbed	• histo-incompatibility (1 pixel of extending distance) • will not be overgrown by other corals
3	Massive Form / Castle-like Faviids	1	1.5	18	No	• the polyp will become dead polyp with a chance of 10% when it is disturbed • whole colony will be overturned and removed from the reef environment by a chance of 1%	• sweeper tentacles (3 pixels of extending distance) • overgrowing
4	Branching / Tabular form Acroporids	3	3	18	Yes	• part of the colony will be broken and removed from the reef environment with a chance of 90%	• overtopping[1] • overgrowing
5	Mushroom-like *Goniopora* or *Alveopora*	1	1.5	18	No	• the polyp will become dead polyp with a chance of 10% when it is disturbed • whole colony will be overturned and removed from the reef environment by a chance of 2%	• sweeper tentacles (5 pixels of extending distance) • will not be overgrown by other corals

[1] The Group 4 corals were set to use overtopping as the first priority competitive mechanism during competition.

3.3.5 Diversity Index and Statistical Analysis

Shannon-Wiener diversity index was used to characterize the species diversity recorded. The equation of Shannon-Wiener diversity index is as follows:

$$\boldsymbol{H} = - \Sigma\, p_i \log p_i$$

where p_i is the proportion of the area covered by coral species i (in pixel) in the simulation. The significance of difference in area cover among different coral groups in different types of simulations was tested using ANOVA, followed by a Tukey test for multiple comparison (Zar, 1996). The data generated at every one-third of a year were used for statistical comparison.

A different index, Shannon-Wiener diversity index, was used for the characterization of the species diversity in computer model rather than the Brillouin index used in investigating zonation pattern of the coral community studied in the field (Section 2.3.3). It was because the initial location of each coral started in the simulation was randomly determined. In addition, the direction for its coral polyps to reproduce asexually and to interact with other coral polyps were also randomly chosen in the model. Therefore, the results obtained from the simulations were based on random samples, while those used for investigating the coral zonation in the field were not. As Shannon-Wiener diversity index was suggested to be used for random samples (Brower *et al.*, 1990), therefore the index was used to characterize the species diversity in this present section.

3.4 Results and Discussion

3.4.1 Growing Behaviour of the Corals

Dynamical behaviour in area cover of a coral, or a coral colony (**Coral** object) of the five different coral groups (Table 3.2) was examined first by running 10 simulations in a stable reef environment with an optimal sea temperature for coral growth. The average rate of area increase of corals from each coral group followed a logistic curve, which is a common population growth form for an organism in a limited environment (Figure 3.8). As it was set in the model, the fastest-growing coral (Coral Group 4) was found to have higher significant average rate of area increase than that of the second fastest-growing coral (Coral Group 2), which in turn had a significantly higher rate of area increase than that of the corals from the slow-growing groups (Coral Groups 1, 3 and 5) (ANOVA with Tukey test for multiple comparison, total DF = 29, groups DF = 2, error DF = 27, $P < 0.05$).

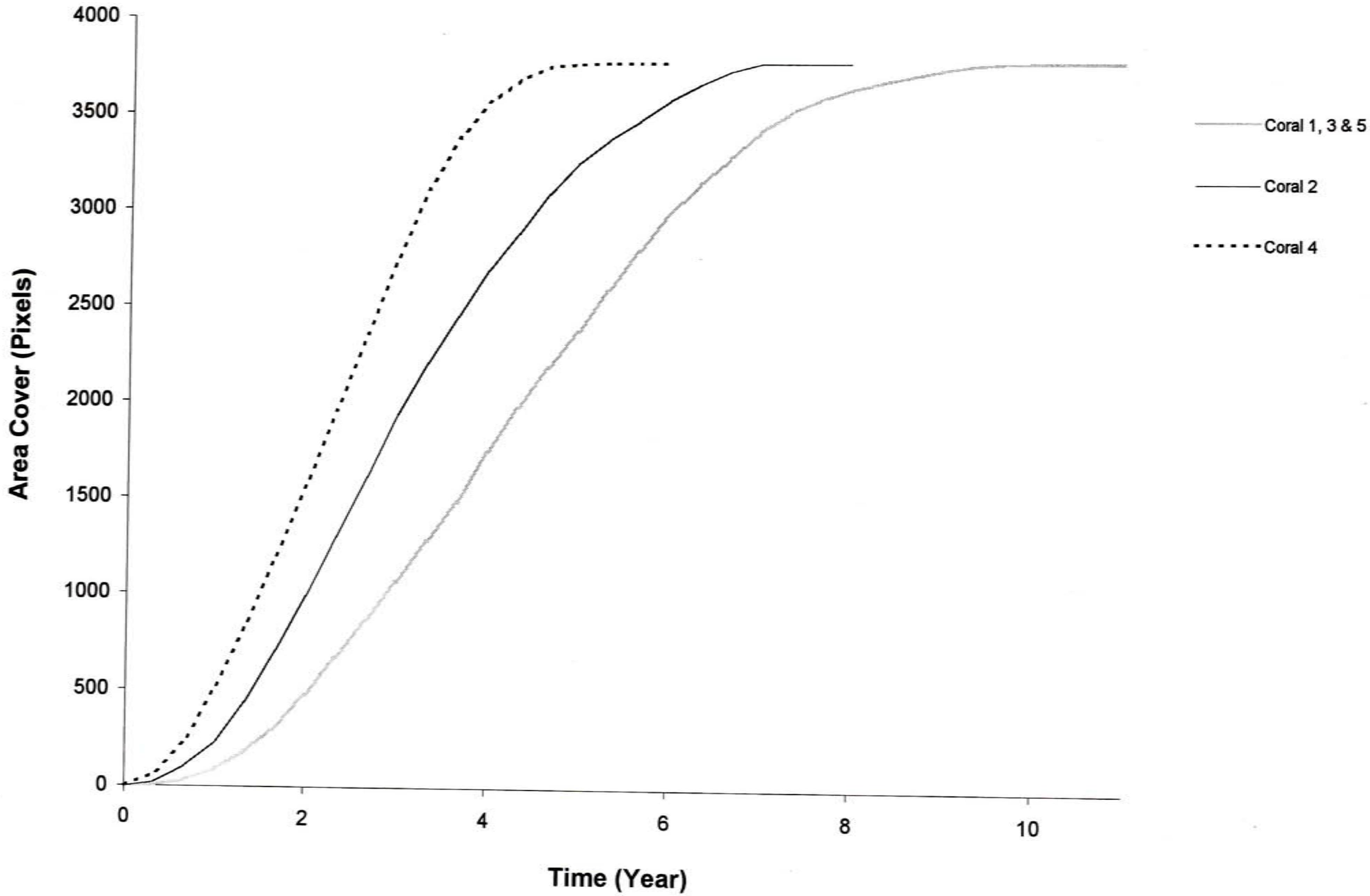
The growing behaviour of each coral from different coral groups was then examined alone in the reef environment, taking into consideration the effect of temperature fluctuation but without any disturbance (0% of area disturbed). This is to investigate the effect of sea temperature set in the reef environment on the rate of area increase for each coral group. Ten simulations were also run and the resulted average change in area cover of the coral from different coral groups is presented in Figure 3.9.

All corals from different coral groups exhibited similar logistic growth form in area change. Their actual average rate of area increase in the reef environment was tabulated in Table 3.3 and was calculated by the following equation:

$$\boxed{dN/dt = rN\,(K - N)/K}$$

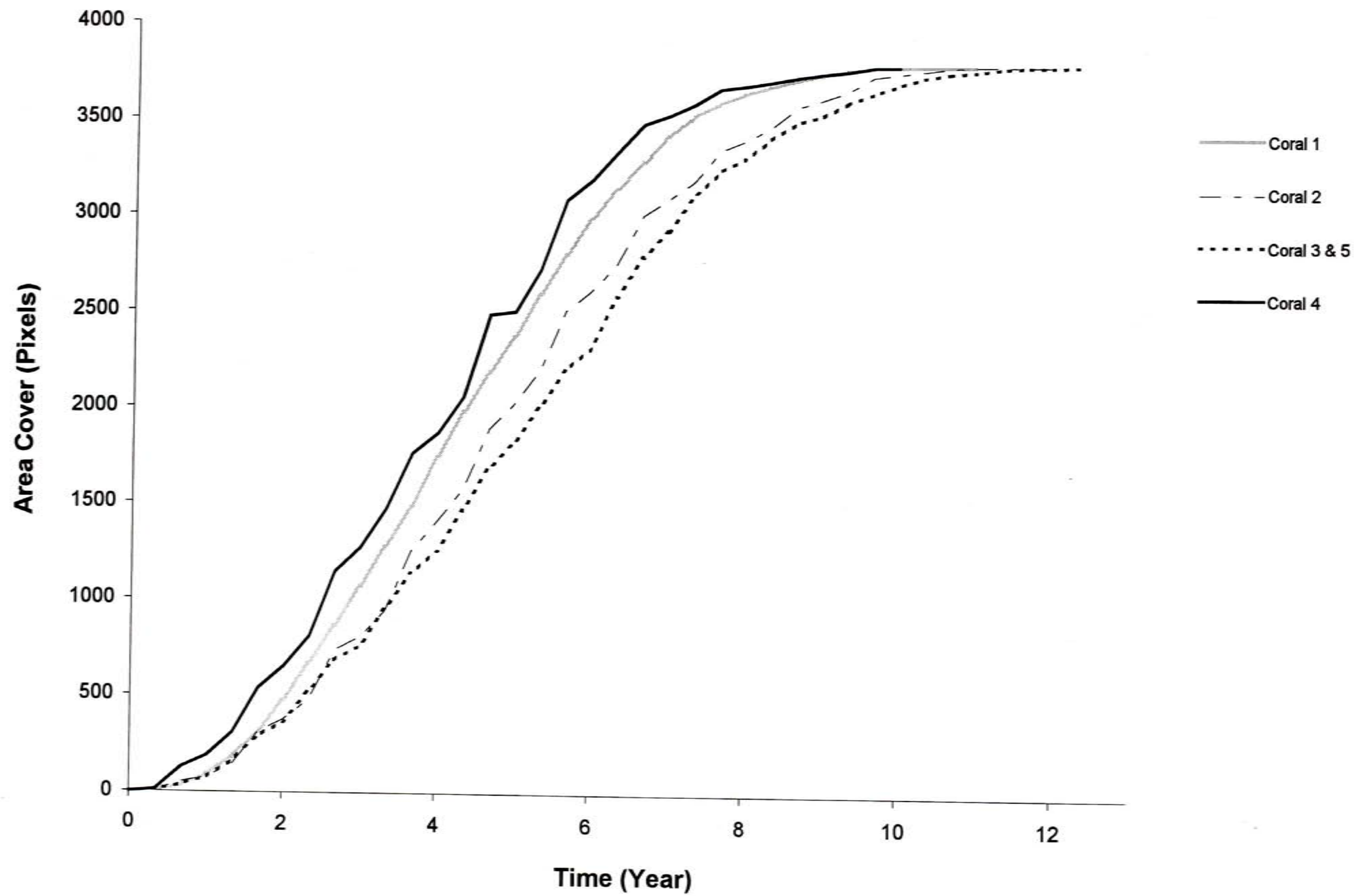
where K is the total reef area and r is the rate of area change per year of the coral from each coral group.

Figure 3.8. Change in area cover of the coral from different coral groups in a stable reef environment with an optimal sea temperature for coral growth. For a description of the different characteristics of each coral group, refer to Table 3.2.



Area Cover (Pixels)
4000
3500
3000
2500
2000
1500
1000
500
0
0
2
4
6
8
10
Time (Year)
Coral 1, 3 & 5
Coral 2
Coral 4

Figure 3.9. Change in area cover of the coral from different coral groups in a stable reef environment with same variation of sea temperature throughout each year. For a description of the different characteristics of each coral group, refer to Table 3.2.



Area Cover (Pixels)
4000
3500
3000
2500
2000
1500
1000
500
0
0
2
4
6
8
10
12
Time (Year)
Coral 1
Coral 2
Coral 3 & 5
Coral 4

Table 3.3. The average rate of area increase of the coral from each coral group in the reef environment with and without the effect of temperature. For a description of the different characteristics of each coral group, refer to Table 3.2.

Coral Group No.	Original Average Rate of Area Increase (pixels/year)	Average Rate of Area Increase with Temperature Effect (pixels/year)
1	7.158	7.158
2	8.952	6.450
3	7.158	5.790
4	13.17	6.906
5	7.158	5.790

The different temperature sensitivity set for each coral group was demonstrated to be effective in influencing their rate of area increase in the reef environment. In the present model, Coral Groups 2 and 4 were those corals with fast-growing habit but sensitive to the temperature change, while Coral Groups 1, 3 and 5 were those corals with slow-growing habit but not sensitive to the temperature change (Table 3.2). The rate of area increase of corals from two temperature-sensitive coral groups (Coral Groups 2 and 4) was found to be significantly decreased by the fluctuation of sea temperature set in the reef environment (two-tailed Student t-test, total DF = 19, groups DF = 1, error DF = 18, $P < 0.05$). However, for those temperature non-sensitive corals (Coral Groups 1, 3 and 5), their overall rate of area increase was not significantly affected by the fluctuating temperature.

3.4.2 Dynamical Behaviour of the Coral Community in Simulation without Disturbance

Change of spatial distribution was observed in the coral community simulated (Figures 3.10 - 3.13). Such change was due to the radial growth of each coral, or each coral colony (**Coral** object) in the reef environment. Dead corals observed in the simulation resulted from the killing activities brought about by various types of interaction that occurred among corals.

Chaotic behaviour was observed in the dynamical structure of the coral community in simulations without disturbance. The trajectory of the change of total area cover of each coral group was found to be different in each simulation. The final total area cover of some coral groups was different in different simulations (Figures 3.14 and 3.15). Precise prediction of the total area cover of each coral group could not therefore be made in the simulated coral community.

Dominance was observed in the coral community simulated when no disturbance occurred in the reef environment. Fast-growing Group 4 corals with overtopping competitive mechanism were found to completely dominate over other corals (Figure

3.16). Except in a few occasions, all corals from the other coral groups died at the end of each simulation because of being overtopped by Group 4 corals (Appendix, Figures A1 - A5). Even if some corals could survive at the end of the simulation, the total area cover of each of these coral groups was significantly lower than that of Group 4 corals (ANOVA with Tukey test for multiple comparison, total DF = 99, groups DF = 4, error DF = 95, $P < 0.001$).

Fast-growing habit with overtopping competitive mechanism, as revealed in this computer model, was one of the powerful strategies for a coral to gain dominance in a stable environment. Fast-growing habit allowed the coral to colonize the reef area immediately once its surrounding space was available. Overtopping competitive mechanism allowed the coral to grow above other corals even when the space was occupied. Such competitive mechanism made "the area of available space" no longer a limiting factor for the coral to grow radially. In addition, corals being overtopped would be killed indirectly (Figure 3.5) in the model. Therefore, the faster rate of colonization of surrounding area brought about by the fast-growing habit, no "available space" limit for radial growth and the indirect killing of other corals brought about by the overtopping competitive mechanism, made the branching / tabular form corals (Coral Group 4) dominant in a simulated stable reef environment. Coral species with such biological characteristics could actually be identified in nature as the dominant species in shallow water coral community (Sorokin, 1993).

Figure 3.10. Spatial distribution of the corals of each coral group in the reef environment at the beginning of a simulation without disturbance. For a description of the different characteristics of each coral group, refer to Table 3.2.

(◎ - Group 1 coral; ● - Group 2 coral; ● - Group 3 coral; ● - Group 4 coral; ● - Group 5 coral; ○ - dead coral)

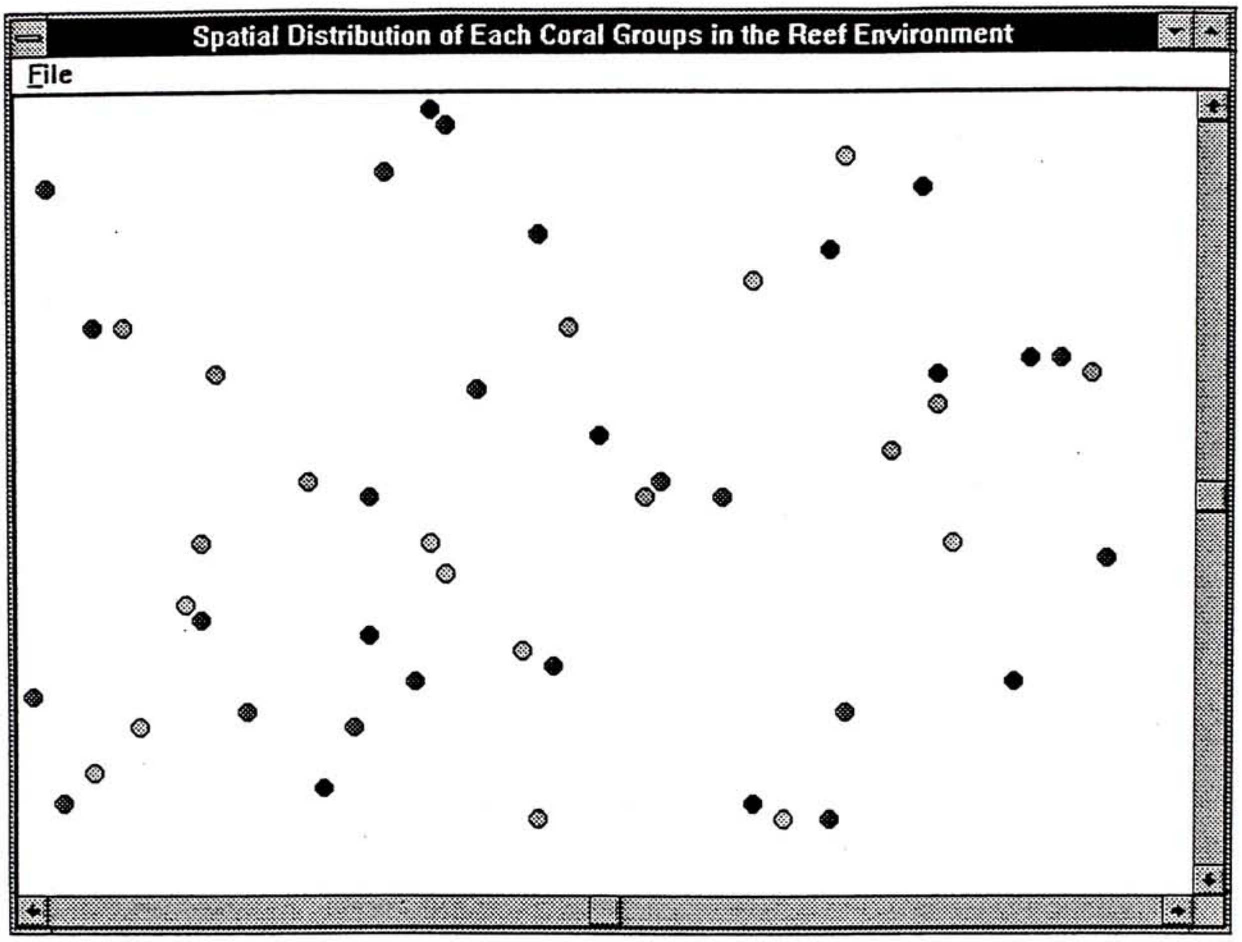

Spatial Distribution of Each Coral Groups in the Reef Environment
File

Figure 3.11. Spatial distribution of the corals of each coral group in the reef environment at 1st year of a simulation without disturbance. For a description of the different characteristics of each coral group, refer to Table 3.2.

(○ - Group 1 coral; ○ - Group 2 coral; ● - Group 3 coral;
● - Group 4 coral; ● - Group 5 coral; ○ - dead coral)

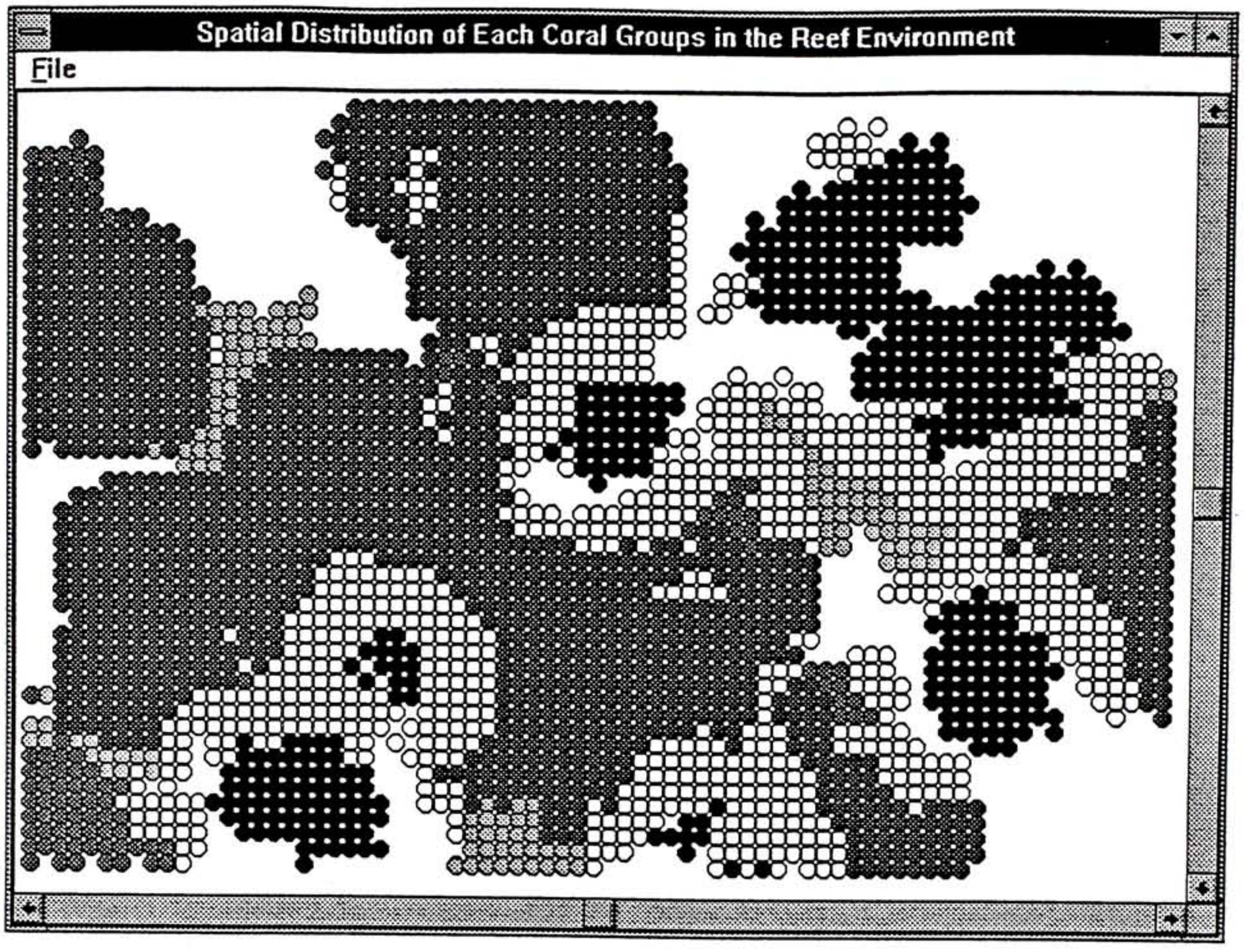

Spatial Distribution of Each Coral Groups in the Reef Environment
File

Figure 3.12. Spatial distribution of the corals of each coral group in the reef environment at 3rd year of a simulation without disturbance. For a description of the different characteristics of each coral group, refer to Table 3.2.

(○ - Group 1 coral; ● - Group 2 coral; ● - Group 3 coral;
● - Group 4 coral; ● - Group 5 coral; ○ - dead coral)

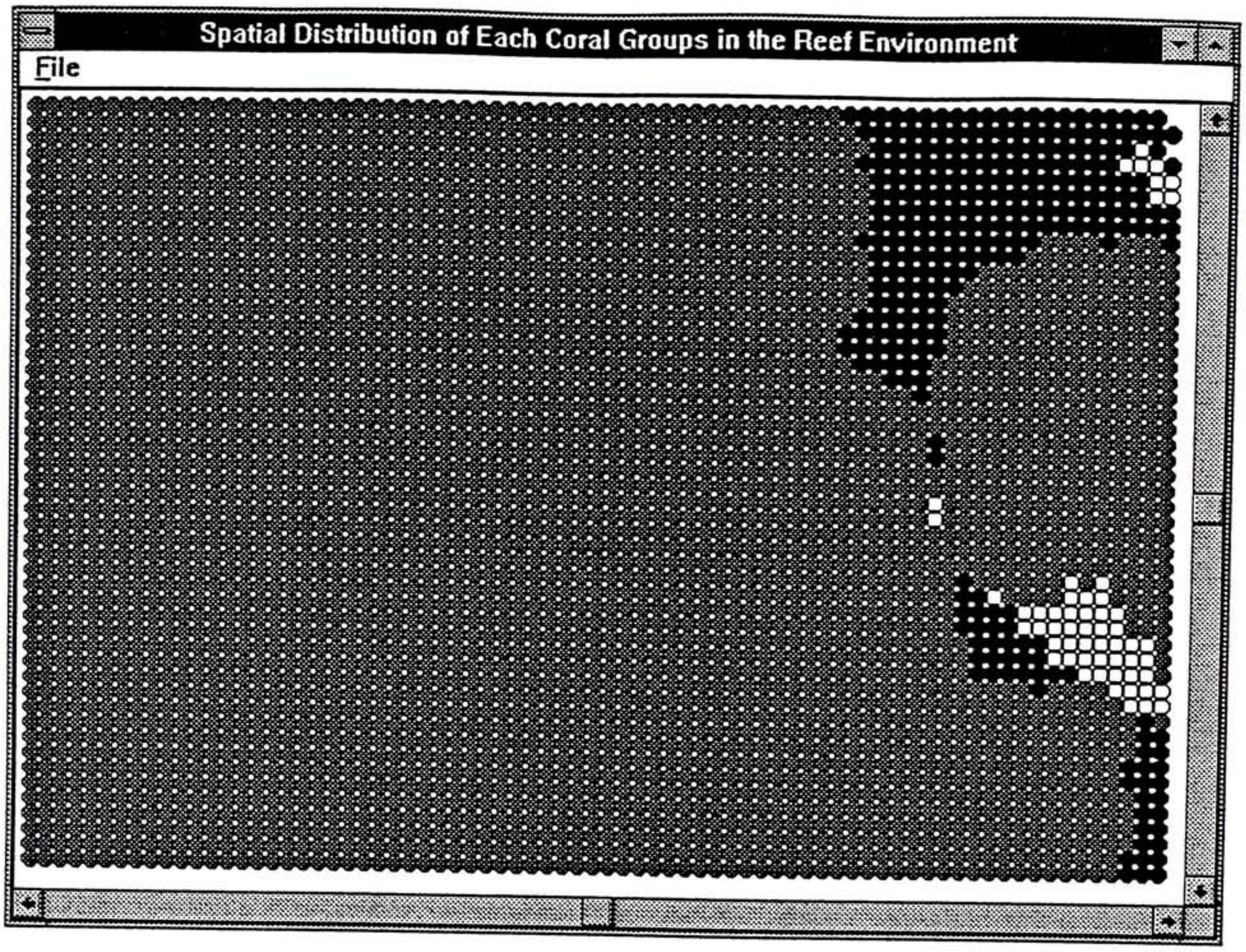

Spatial Distribution of Each Coral Groups in the Reef Environment
File

Figure 3.13. Spatial distribution of the corals of each coral group in the reef environment at the end of a simulation without disturbance. For a description of the different characteristics of each coral group, refer to Table 3.2.

(○ - Group 1 coral; ● - Group 2 coral; ● - Group 3 coral; ● - Group 4 coral; ● - Group 5 coral; ○ - dead coral)

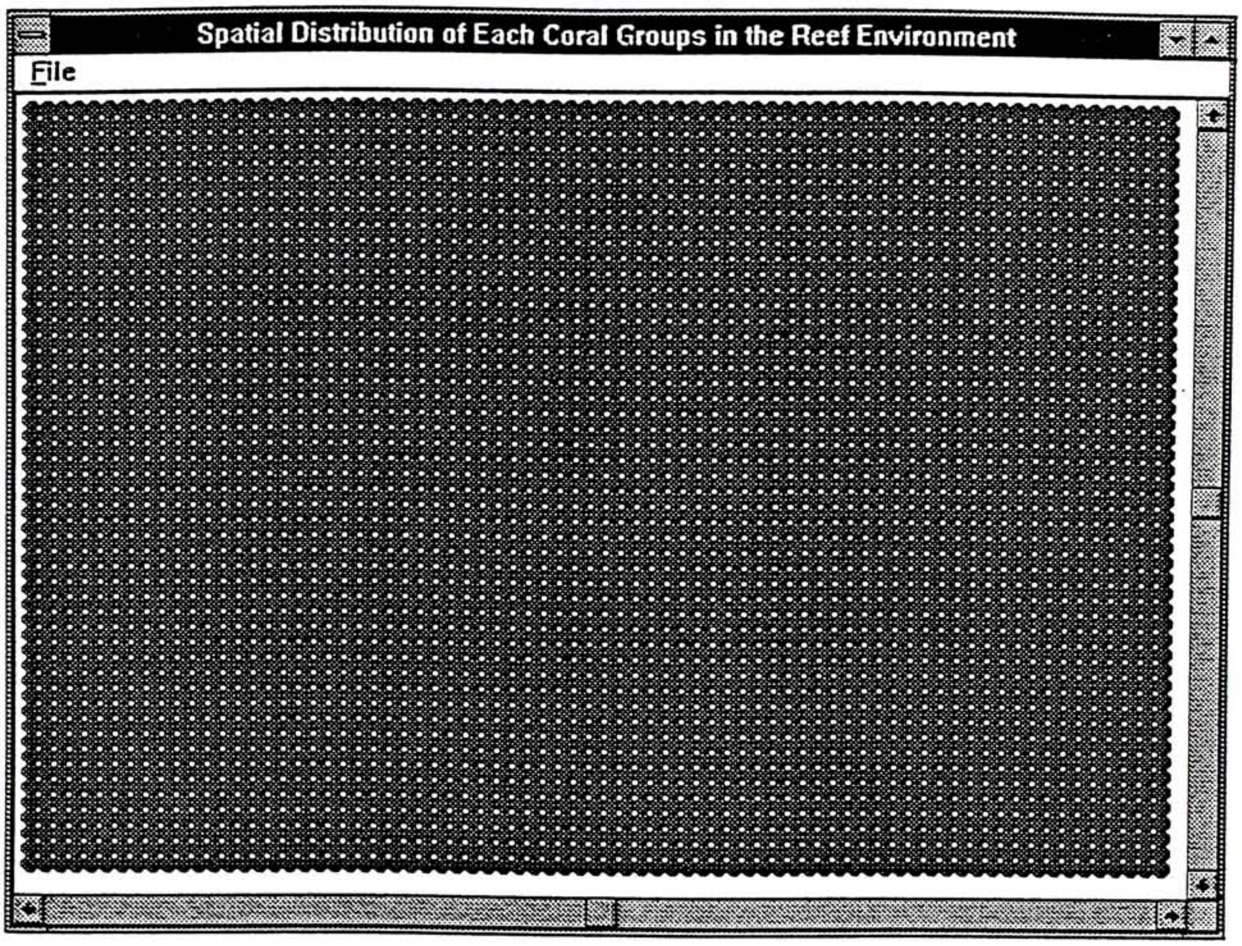

Spatial Distribution of Each Coral Groups in the Reef Environment
File

Figure 3.14. Change in total area cover of all branching / tabular growth form acroporids (Group 4 corals) in each simulation without disturbance.

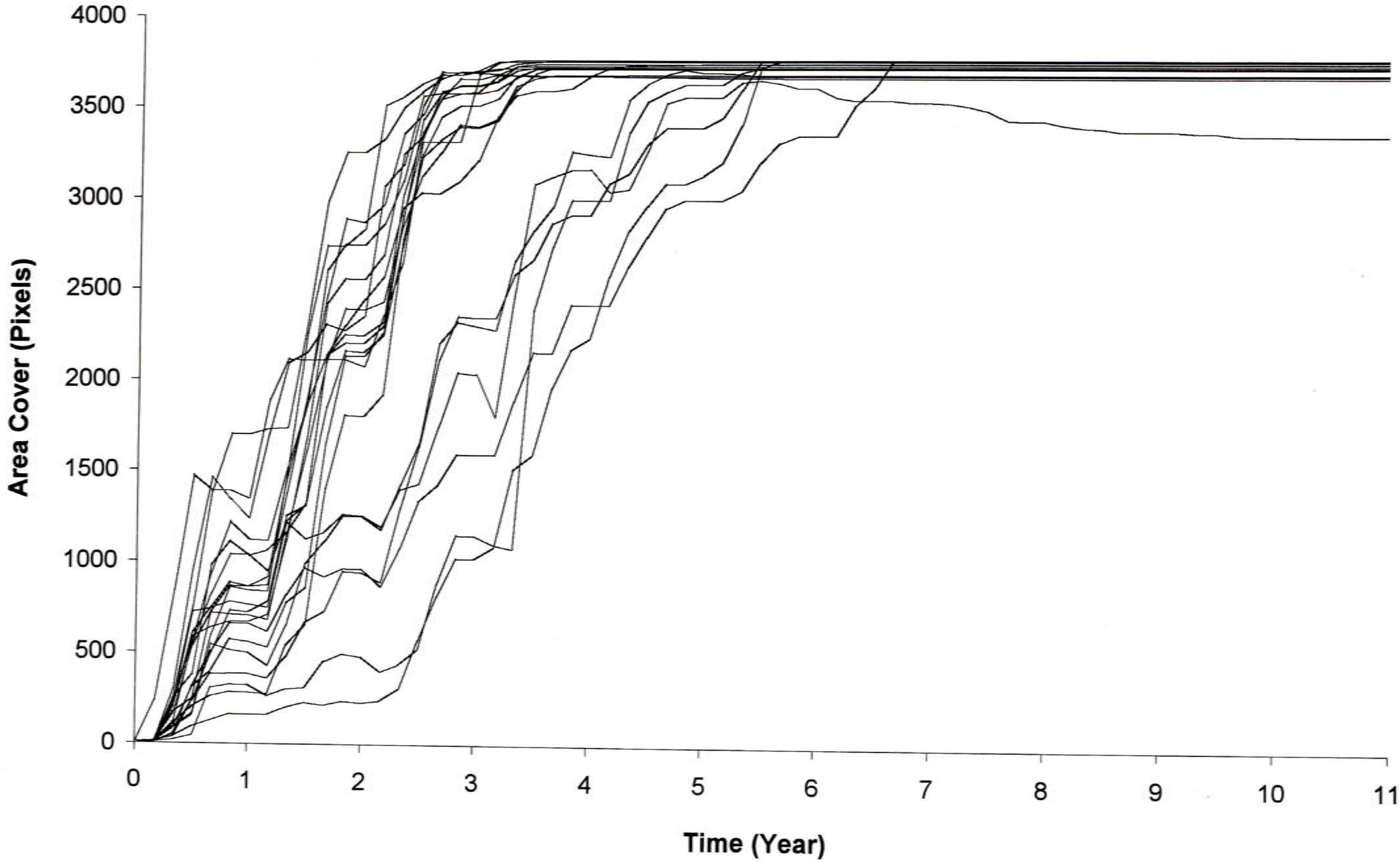

Area Cover (Pixels)
4000
3500
3000
2500
2000
1500
1000
500
0
0
1
2
3
4
5
6
7
8
9
10
11
Time (Year)

Figure 3.15. Change in total area cover of all massive-form / castle-like faviids (Group 3 corals) in each simulation without disturbance.

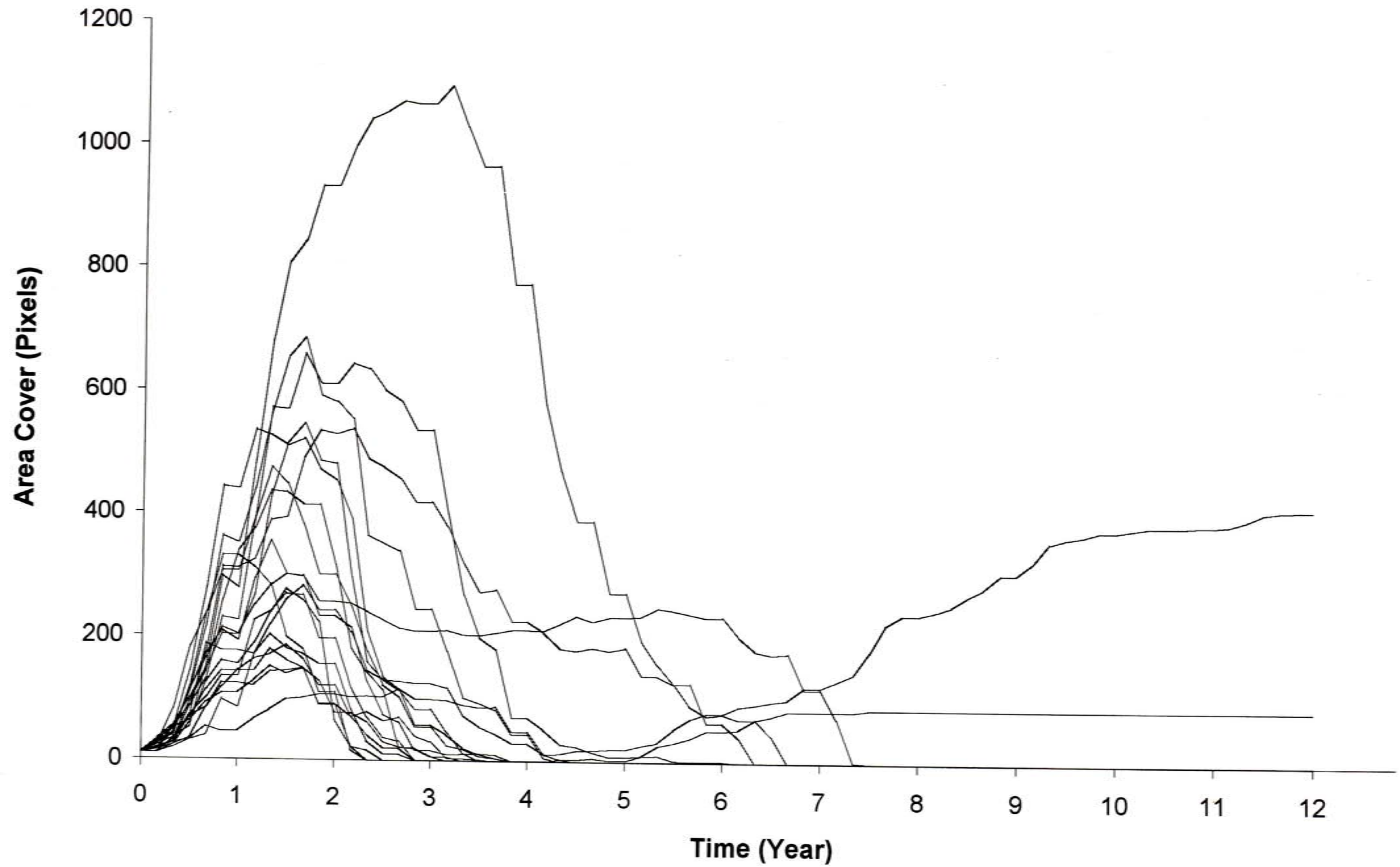
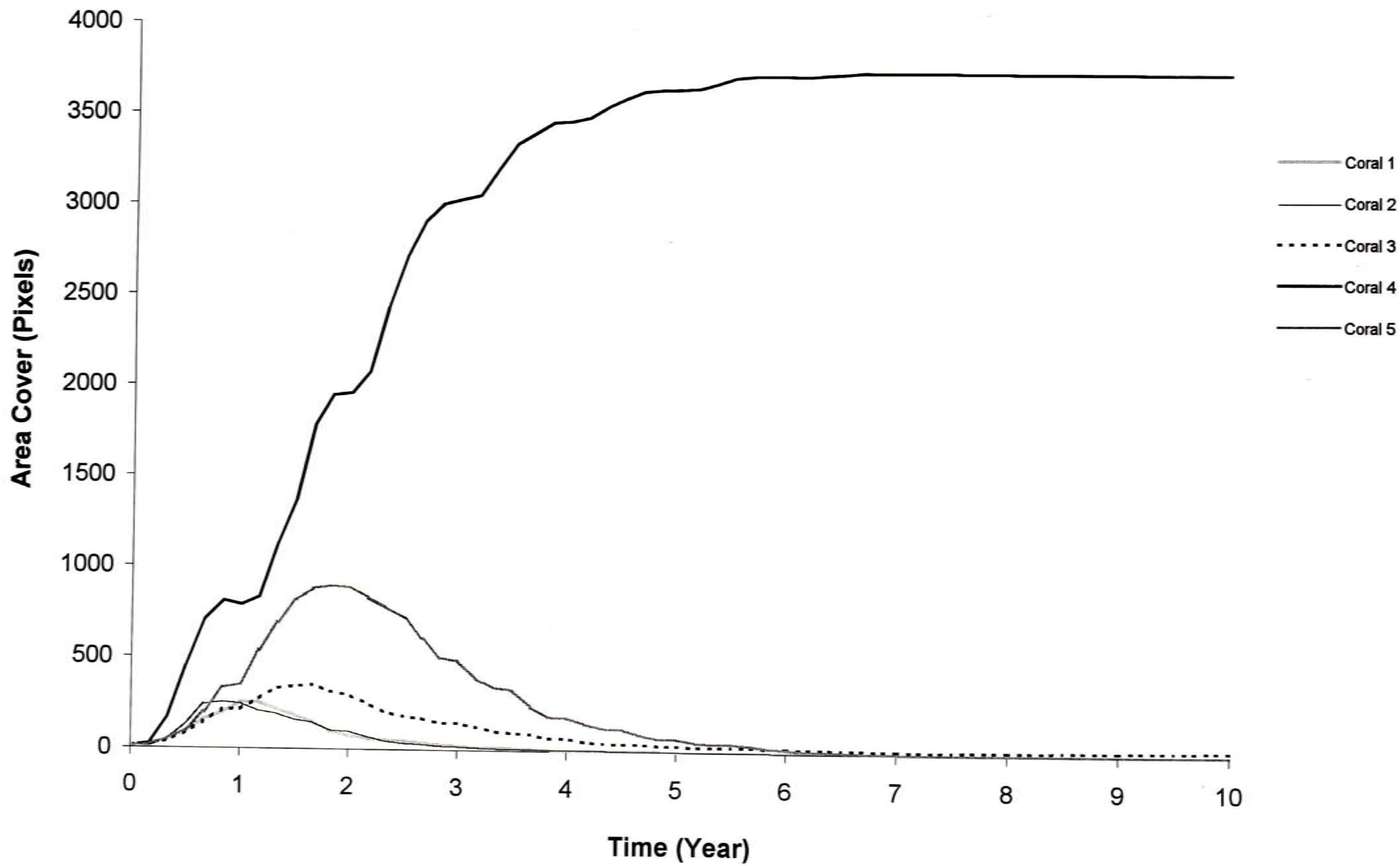

Area Cover (Pixels)
0
200
400
600
800
1000
1200
0
1
2
3
4
5
6
7
8
9
10
11
12
Time (Year)

Figure 3.16. Average change in total area cover of each coral group in the simulation without any disturbance. For a description of the different characteristics of each coral group, refer to Table 3.2.


Area Cover (Pixels)
4000
3500
3000
2500
2000
1500
1000
500
0
0
1
2
3
4
5
6
7
8
9
10
Time (Year)
Coral 1
Coral 2
Coral 3
Coral 4
Coral 5

3.4.3 Dynamical Behaviour of the Simulated Coral Community with Disturbance

3.4.3.1 General Dynamical Behaviour of the Coral Community with Disturbance

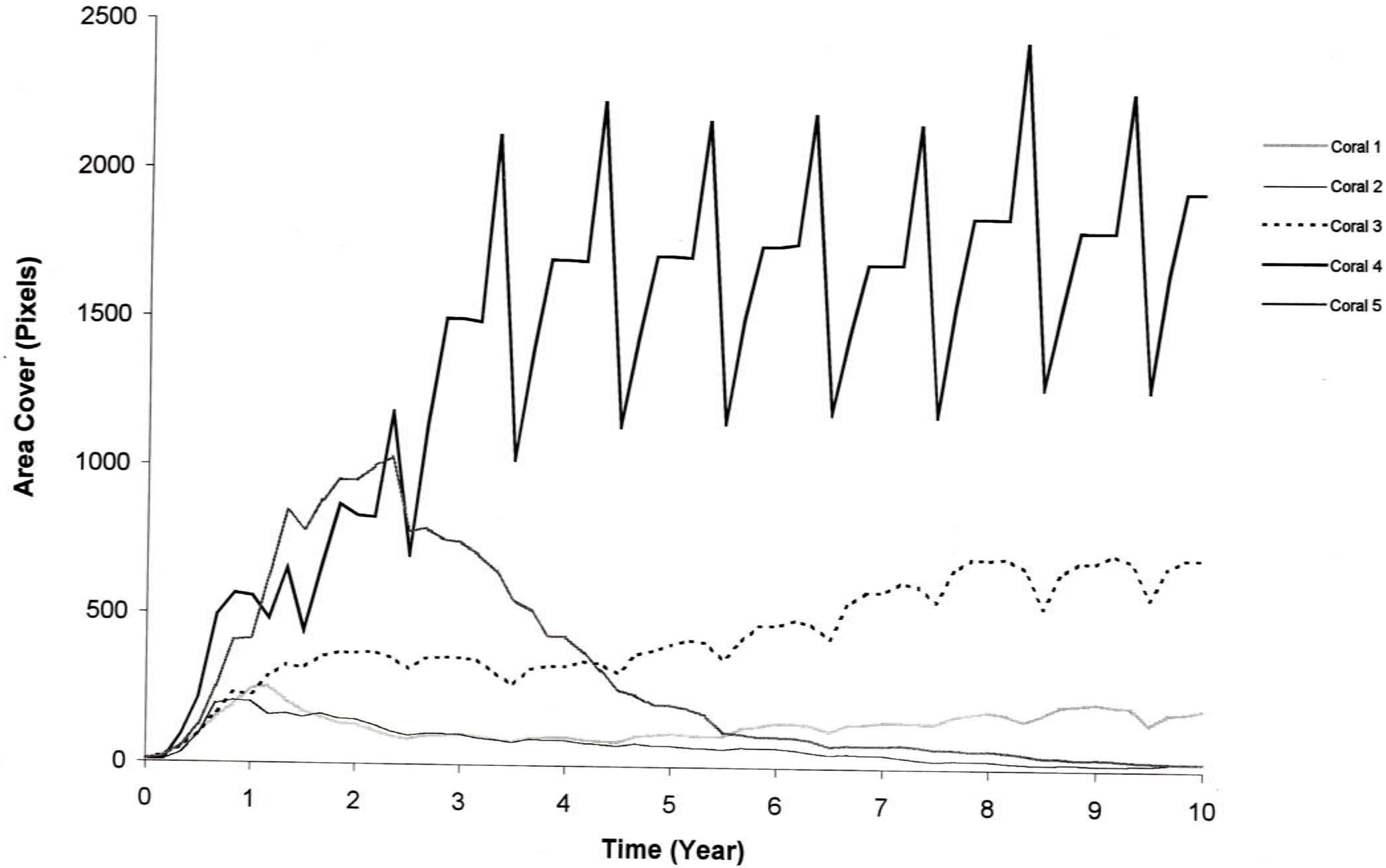
The total area cover of each coral group in the simulated community exhibited periodic behaviour when exposed to disturbance (Figures 3.17 - 3.20). Such periodic behaviour was due to the regular occurrence of disturbance annually. When a disturbance occurred, the area cover of each coral or each coral colony (**Coral** object) would be decreased since each coral could have a chance of being killed in the disturbance. The area cover of each coral would then increase after the disturbance as these corals were set to grow continuously throughout the year. Their area cover would be decreased again when the next disturbance occurred, and resulted in a periodic change in their area cover.

Amplitude of the fluctuation of total area cover was different among coral groups, and such phenomenon was due to different sensitivities of coral groups towards disturbance. Only Coral Group 4 (branching / tabular form coral group) was found to have a large fluctuation of total area cover in all simulations. This was because this group of corals was the most sensitive coral group (highest chance of being killed in disturbance) in the coral community simulated and was dominating over other coral groups in stable reef environment (Section 3.4.2). Fluctuation in total area cover of this coral group could only be due to its high sensitivity towards disturbance. This argument was further supported by the relatively low level of fluctuation in total area cover found in other less disturbance sensitive coral groups (i.e. Coral Groups 1, 2, 3 and 5) in the simulations.

Amplitude of the fluctuation of total area cover was also found to be different under different degrees of disturbance. Larger fluctuation was generally observed for those slow-growing corals (Group 1, 3 and 5 corals) in the simulations with intermediate disturbance level, while this was noticed for faster growing corals (Group 2 corals) in the simulations with high disturbance level. For Group 4 corals, large fluctuation was found in both simulations with low and intermediate disturbance levels (Figures 3.21 - 3.25). Such responses observed for Groups 1, 2, 3 and 5 corals were mainly due to the higher area cover obtained in those simulations for these coral groups. Since for each coral group with more area covered, chances of being killed in a disturbance would become higher. A larger fluctuation in the total area cover could thus be observed.

Similar interpretation can be applied for Group 4 corals. Since Group 4 corals covered a large area in the simulations with low disturbance level, therefore their chance of being disturbed should be higher in that type of simulations. In addition, as area being disturbed in the reef environment was set directly proportional to the level of disturbance, chance of corals being disturbed should be higher when the degree of disturbance increased. Therefore, even though the total area cover of Group 4 corals in the simulations with intermediate disturbance level was not as high as that observed in the simulations with low disturbance level, the increase in the area of the reef being disturbed in the simulations with intermediate disturbance would still lead to a large fluctuation in the total area cover of Group 4 corals. However, since the total area cover of Group 4 corals was kept low in the simulations with high level of disturbance, their area fluctuation would not be as great as that found in the simulations with low and intermediate levels of disturbance.

Figure 3.17. Average change in total area cover of each coral group in the simulation under fixed time low level of disturbance (10% of area being disturbed each time). For a description of the different characteristics of each coral group, refer to Table 3.2.



Area Cover (Pixels)
2500
2000
1500
1000
500
0
0
1
2
3
4
5
6
7
8
9
10
Time (Year)
Coral 1
Coral 2
Coral 3
Coral 4
Coral 5

Figure 3.18. Average change in total area cover of each coral group in the simulation under fixed time intermediate level of disturbance (25% of area being disturbed each time). For a description of the different characteristics of each coral group, refer to Table 3.2.

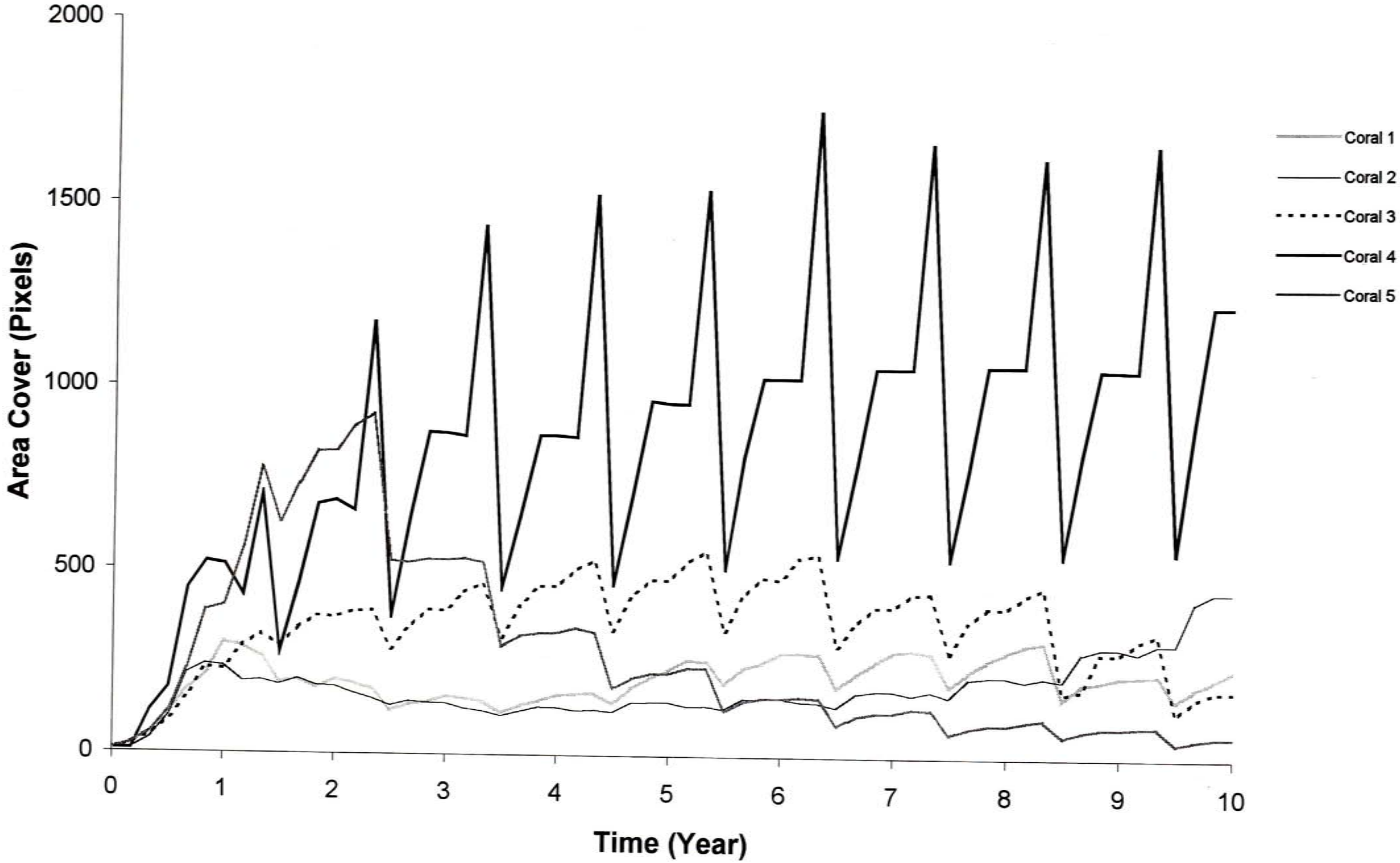
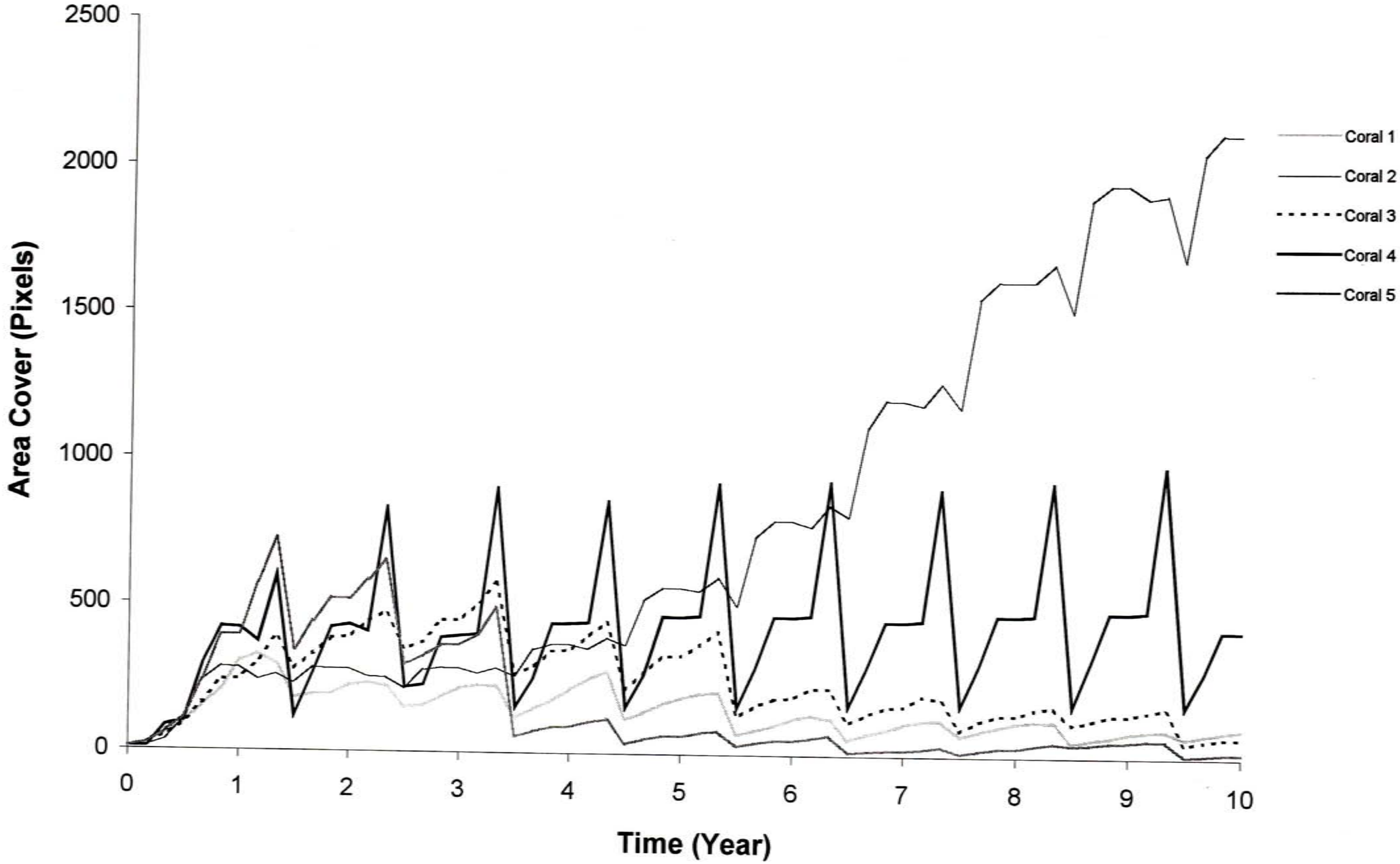

Area Cover (Pixels)
2000
1500
1000
500
0
0
1
2
3
4
5
6
7
8
9
10
Time (Year)
Coral 1
Coral 2
Coral 3
Coral 4
Coral 5

Figure 3.19. Average change in total area cover of each coral group in the simulation under fixed time high level of disturbance (50% of area being disturbed each time). For a description of the different characteristics of each coral group, refer to Table 3.2.



Area Cover (Pixels)
2500
2000
1500
1000
500
0
0
1
2
3
4
5
6
7
8
9
10
Time (Year)
Coral 1
Coral 2
Coral 3
Coral 4
Coral 5

Figure 3.20. Average change in total area cover of each coral group in the simulation under random time intermediate level of disturbance (25% of area being disturbed each time). For a description of the different characteristics of each coral group, refer to Table 3.2.

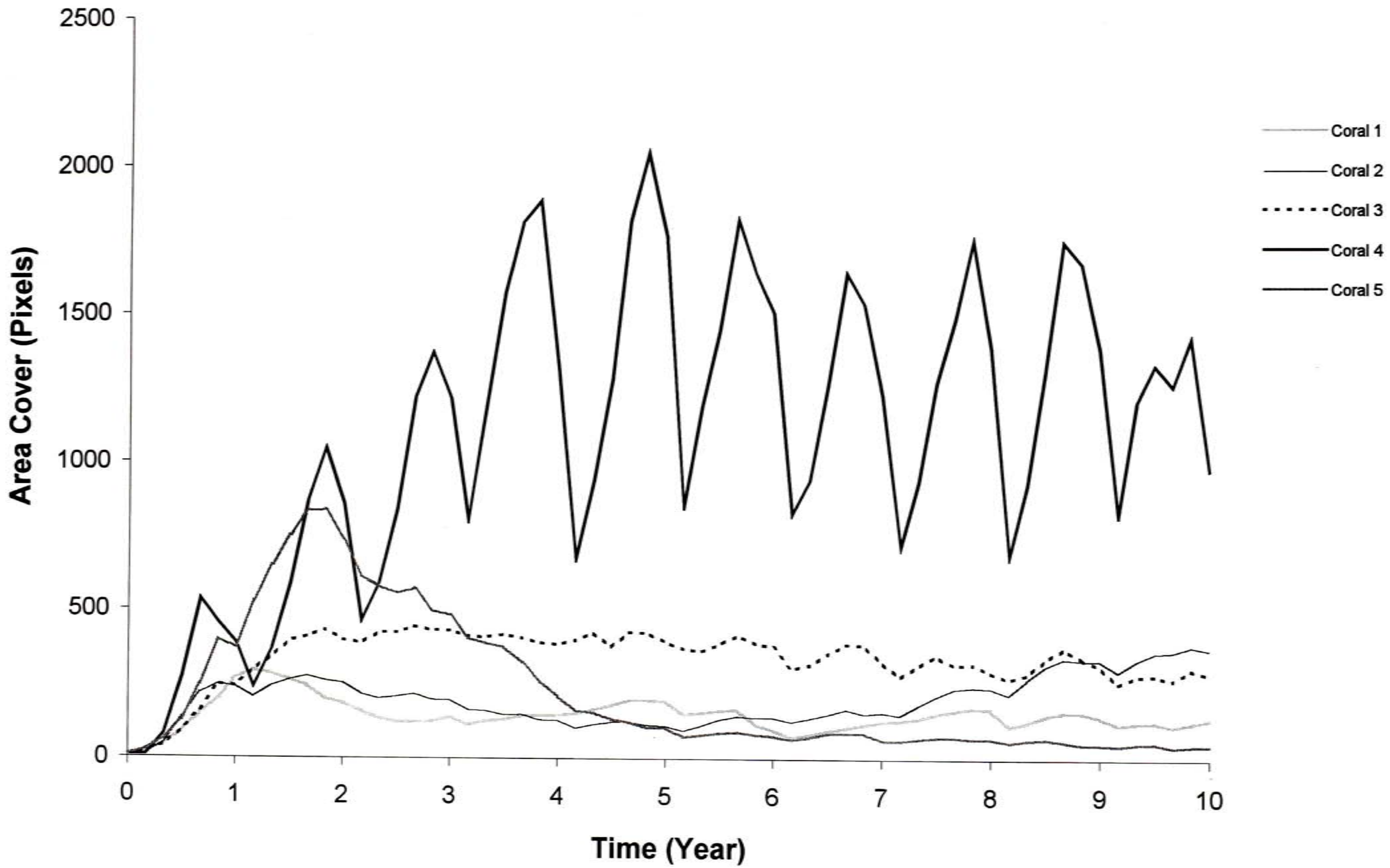
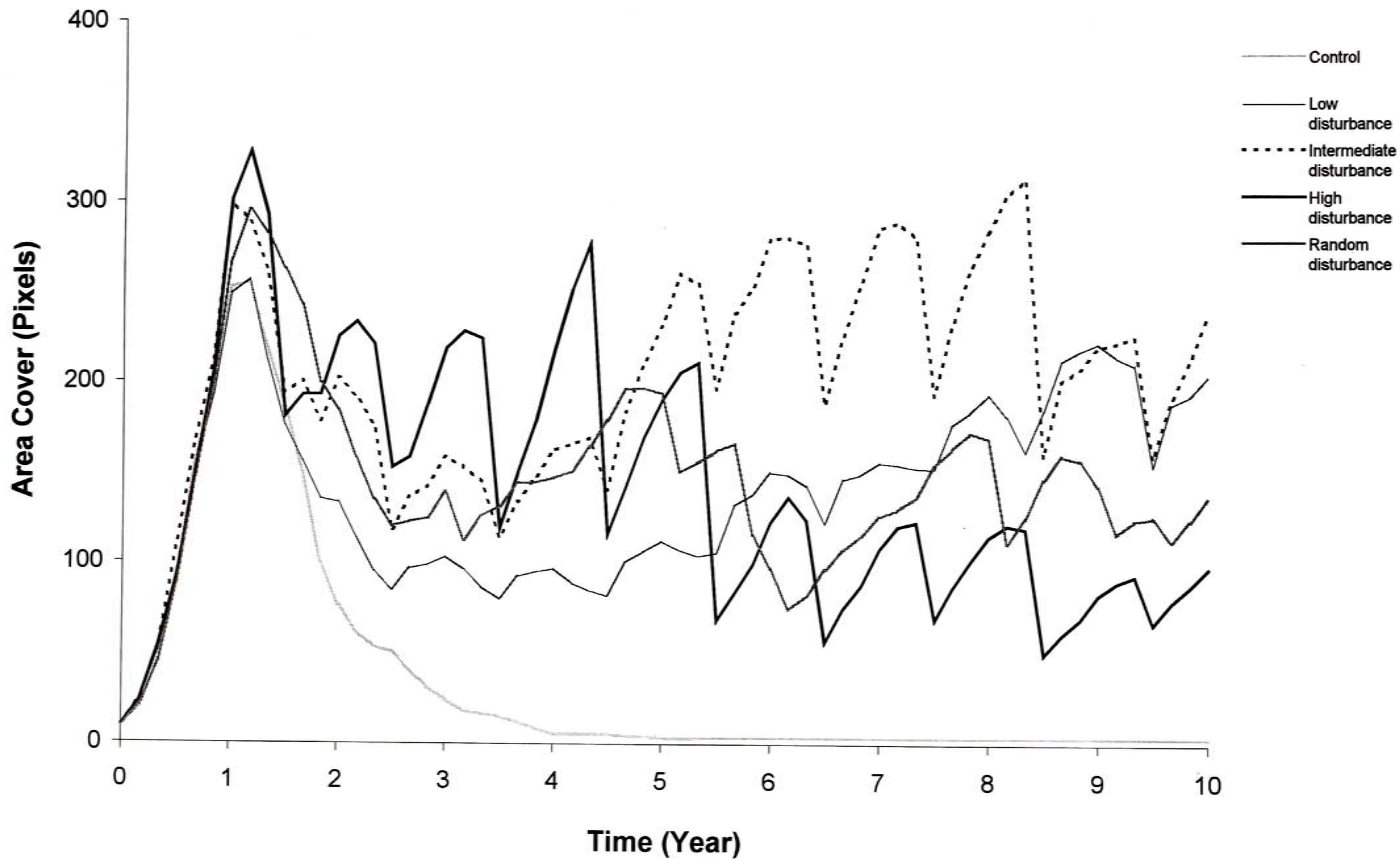

Area Cover (Pixels)
2500
2000
1500
1000
500
0
0
1
2
3
4
5
6
7
8
9
10
Time (Year)
Coral 1
Coral 2
Coral 3
Coral 4
Coral 5

Figure 3.21. Average change in total area cover of all massive form *Porites lobata* (Group 1 corals) in the simulation under different levels of disturbance.



400
300
200
100
0
Area Cover (Pixels)
0
1
2
3
4
5
6
7
8
9
10
Time (Year)
Control
Low disturbance
Intermediate disturbance
High disturbance
Random disturbance

Figure 3.22. Average change in total area cover of all foliaceous *Pavona decussata* (Group 2 corals) in the simulation under different levels of disturbance.

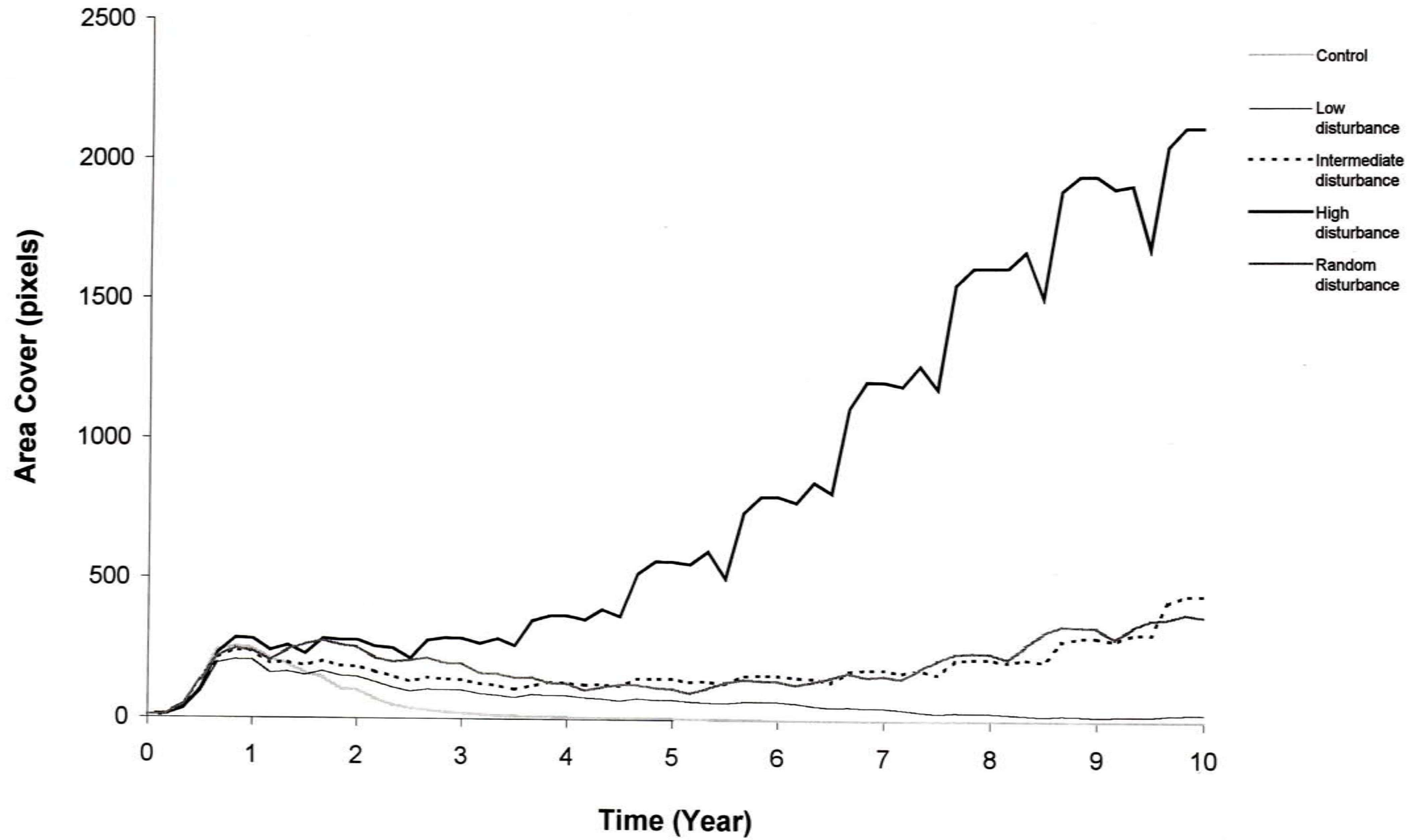

Area Cover (pixels)
2500
2000
1500
1000
500
0
0
1
2
3
4
5
6
7
8
9
10
Time (Year)
Control
Low disturbance
Intermediate disturbance
High disturbance
Random disturbance

Figure 3.23. Average change in total area cover of all massive form / castle-like faviids (Group 3 corals) in the simulation under different levels of disturbance.

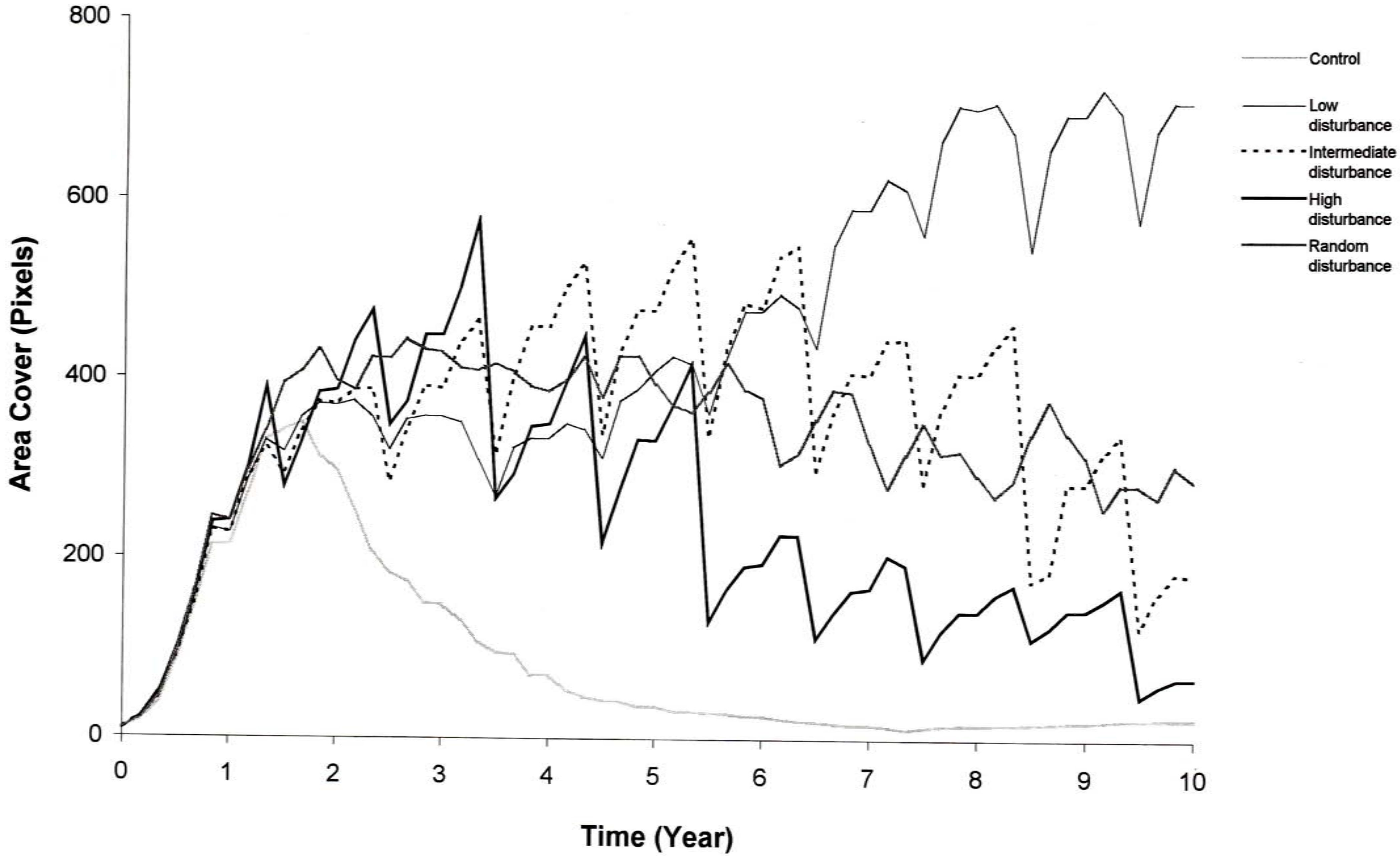

Area Cover (Pixels)
800
600
400
200
0
Time (Year)
0
1
2
3
4
5
6
7
8
9
10
Control
Low disturbance
Intermediate disturbance
High disturbance
Random disturbance

Figure 3.24. Average change in total area cover of all branching / tabular form acroporids (Group 4 corals) in the simulation under different levels of disturbance.

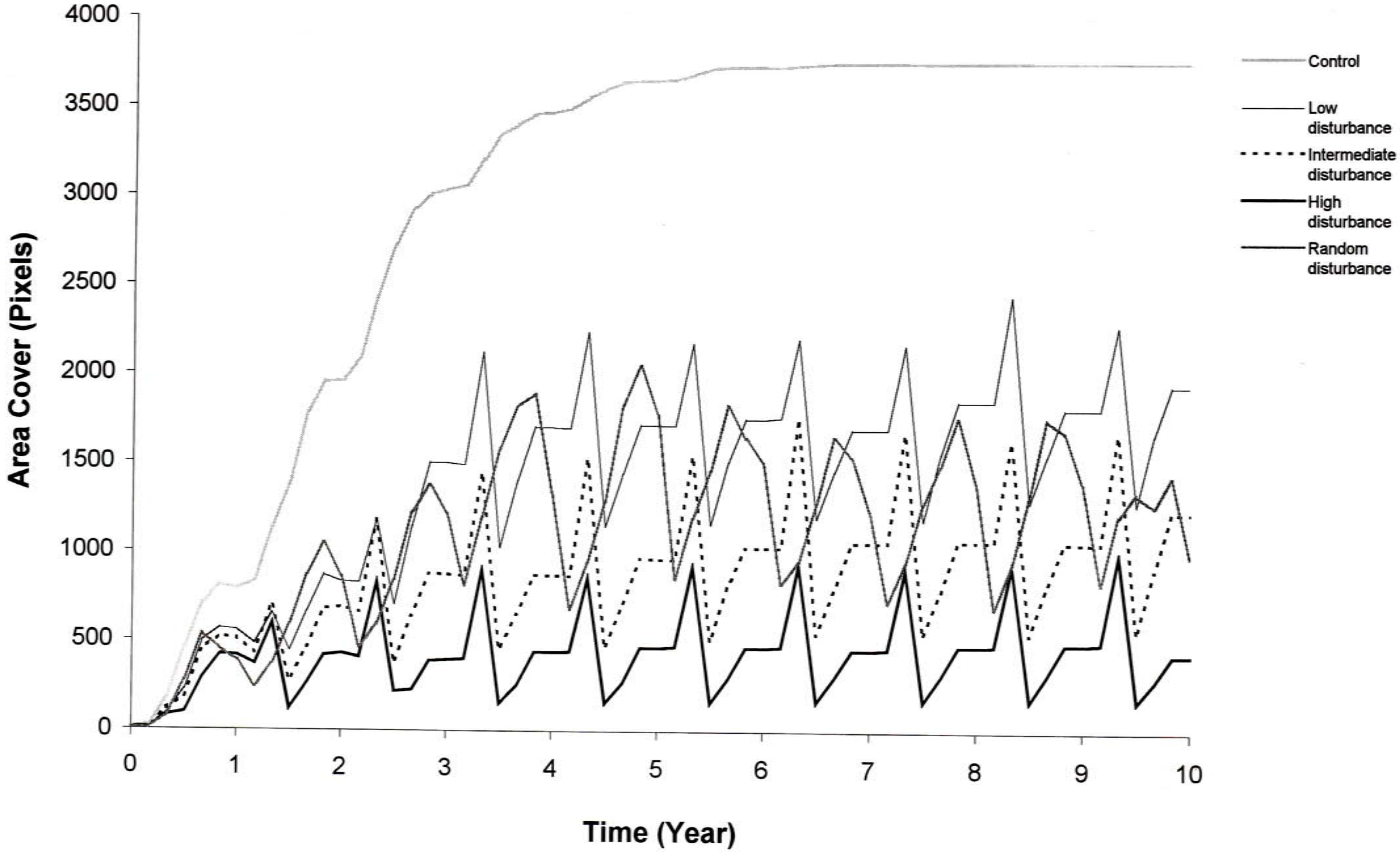
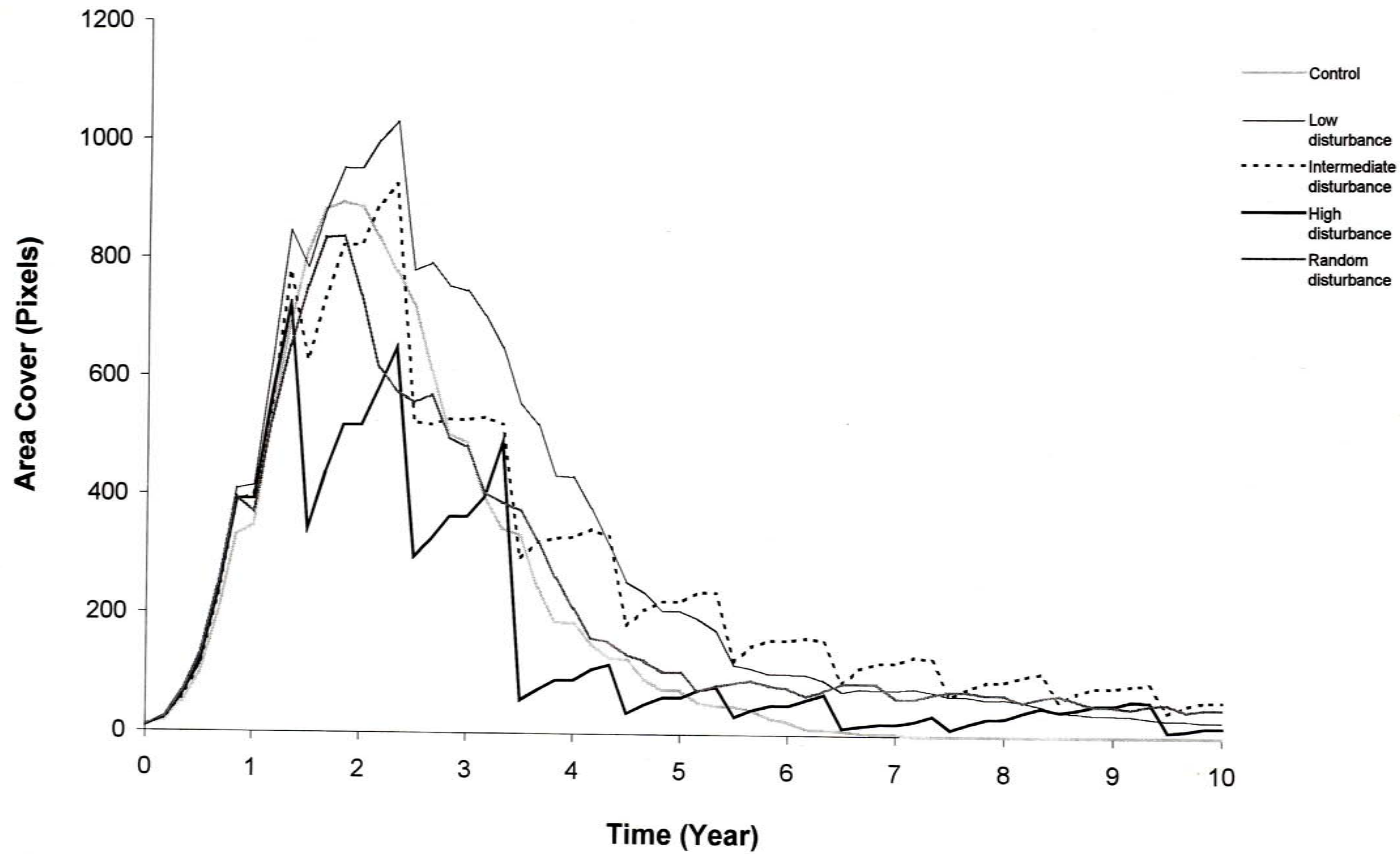

Area Cover (Pixels)
4000
3500
3000
2500
2000
1500
1000
500
0
0
1
2
3
4
5
6
7
8
9
10
Time (Year)
Control
Low disturbance
Intermediate disturbance
High disturbance
Random disturbance

Figure 3.25. Average change in total area cover of all mushroom-like *Goniopora* or *Alveopora* (Group 5 corals) in the simulation under different levels of disturbance.


Area Cover (Pixels)
1200
1000
800
600
400
200
0
0
1
2
3
4
5
6
7
8
9
10
Time (Year)
Control
Low disturbance
Intermediate disturbance
High disturbance
Random disturbance

3.4.3.2 Disturbance Effects on Species Dominance

Disturbance was found to have a striking effect on the dynamical structure of the coral community simulated. Species dominance was altered by different degrees of disturbance that occurred at a fixed time. Group 2 corals (foliaceous form coral group) had the second fastest radial growing rate and intermediate sensitivity to disturbance, while the dominant fast-growing Group 4 corals were the most sensitive corals towards disturbance. A random portion of its colony has a 90% chance of being broken at the point of being disturbed. Group 2 corals, although less dominant in simulations with low and intermediate disturbance levels and simulation without any disturbance, became dominant in the community under high level of disturbance (Figures 3.17 - 3.20). Such results indicated that the ability to withstand disturbance was one of the necessary strategies for a coral to gain dominance in a very unstable environment.

The dominance of a less disturbance sensitive coral in a disturbed environment was found to be affected also by their growing form set in the model. The colonies of massive form, mushroom-like or castle-like corals (Coral Groups 1, 3 and 5) had a small chance of being overturned and killed during disturbance (Table 3.2). On the other hand, the foliaceous corals (Coral Group 2), would be broken only at the point of being disturbed. Under increasing degree of disturbance, i.e., when the area being disturbed increased, the chance of massive form, mushroom-like or castle-like corals being overturned also increased. As overturning will cause the whole colony to die in the model, the chance of massive form, mushroom-like or castle-like corals being killed under high level of disturbance would thus become greater than that for foliaceous form corals, even though the former was less sensitive to disturbance than the latter.

The intermediate fast growth rate of foliaceous corals (Group 2 corals) also contributed to their dominance in the highly disturbed environment. As the total area of the branching / tabular form corals (Coral Group 4) was kept at a low level by the high level of disturbance, many free space became available for other coral colonies to grow in. Since the growth rate of foliaceous corals (Coral Group 2) was faster than that of other corals, it could therefore colonize the available space faster and out-compete other slow-growing corals. As a result, the growing behaviour of foliaceous corals (Coral Group 2), and its integrated strategies in responding to disturbance made them dominant in the simulated coral community under highly disturbed environment.

3.4.3.3 Disturbance Effects on Each Coral

Dominant branching / tabular form corals (Coral Group 4) were found to be significantly sensitive to different degrees of disturbance. Their total area cover was found fluctuating around an equilibrium level when disturbance occurred (Figure 3.24). The equilibrium level, around which branching / tabular corals (Coral Group 4) was fluctuating, had significantly decreased when the disturbance level increased (ANOVA with Tukey test for multiple comparison, total DF = 99, groups DF = 4, error DF = 95, $P < 0.05$). Disturbance thus has prominent effect on the population dynamics of those dominant and disturbance sensitive coral groups in the coral community simulated.

Disturbance was also found to affect the total area cover of the less dominant coral groups in the community (Figures 3.22 - 3.25). Groups 1, 2 and 3 corals had increased their final area cover significantly (ANOVA with Tukey test for multiple comparison, total DF = 99, groups DF = 4, error DF = 95, $P < 0.05$) at the end of the simulation when the disturbance level was either low or intermediate. Such phenomenon was due to the total area cover of branching / tabular corals (Coral Group 4) being significantly lowered by the disturbance. Free space was thus kept available continuously in the reef environment for those less dominant corals to colonize.

However, when the disturbance level was too high, all the less dominant corals (except Group 2 corals) were kept at a low level of total area cover as well. The chances for massive form, mushroom-like or castle-like of corals, (Coral Groups 1, 3 and 5) to be overturned were increased by increasing intensity of disturbance (Section 3.4.3.2). The dominance of foliaceous corals (Coral Group 2) was observed under high level of disturbance and the occurrence of their dominance has been explained in section 3.4.3.2.

3.4.3.4 Disturbance Effects on Species Diversity

Species diversity was also affected by different degrees of disturbance (Figure 3.26). Species diversity was found fluctuating around an equilibrium level at the end of each simulation in every disturbance level. The equilibrium level of the species diversity in all disturbance levels was found significantly higher than that observed in the simulation without any disturbance (ANOVA with Tukey test for multiple comparison, total DF = 99, groups DF = 4, error DF = 95, $P < 0.001$). This was because frequent disturbance has kept on damaging the originally dominant branching / tabular form corals (Coral Group 4) in the simulating environment. As a result, the reef environment was not overwhelmed by the branching / tabular form corals (as the case in simulation without disturbance, Figure 3.16) and the other least dominant corals were given a free space to colonize.

Significant higher equilibrium level of species diversity (ANOVA with Tukey test for multiple comparison, total DF = 99, groups DF = 4, error DF = 95, $P < 0.05$) was found in simulation with intermediate disturbance level (25% of area being disturbed). Such behaviour of the simulating coral community could be understood since the total area cover of the original dominant fast-growing Group 4 corals was kept low in the intermediate level of disturbance. The opening up of adequate amount of space, originally occupied by Group 4 corals, thus allowed the colonization of other less dominant but disturbance-resistant corals (Coral Groups 1, 2, 3 and 5). The latter, which were normally lost in competition for space or were killed by the dominant branching / tabular form corals (Coral Group 4) in a stable environment, were able to survive in this unstable reef environment. Species diversity can thus be maintained at a comparatively high level at the end of simulation under intermediate level of disturbance.

However, species diversity was lower under conditions of low and high levels of disturbance. This was because in both disturbance levels, dominant group of corals still appeared and out-competed other less dominant groups of corals (Figures 3.17 and 3.19). The resulting species diversity was thus lower than that found under the condition of intermediate disturbance.

A coral community simulated in this modelling study was found to have significantly higher species diversity in intermediate level of disturbance. Such behaviour observed agreed well with the "intermediate disturbance hypothesis" described by Connell (1978). "Intermediate disturbance hypothesis" proposed that high diversity is normally found in the complex ecological systems, such as coral reef community or tropical rainforest, which are maintained by disturbance operating at intermediate levels (Connell, 1978). Such hypothesis considered the possible mechanisms responsible for maintaining the diversity in the complex ecological systems.

Many ecological studies have since conducted to support "intermediate disturbance hypothesis". Hinds and Ballantine (1987) have demonstrated that the non-selective feeding behaviour of a threespot damselfish, *Stegastes planifrons,* has provided an "intermediate disturbance" effect to maintain a greater algal species richness in the algal lawn communities. Later study by Owen (1988) has also shown that the rodent diversity was highest at the intermediate level of net above-ground primary productivity. In addition, Collins *et al.* (1995) have recently found that highest plant species composition occurred in a site with intermediate frequency of burning.

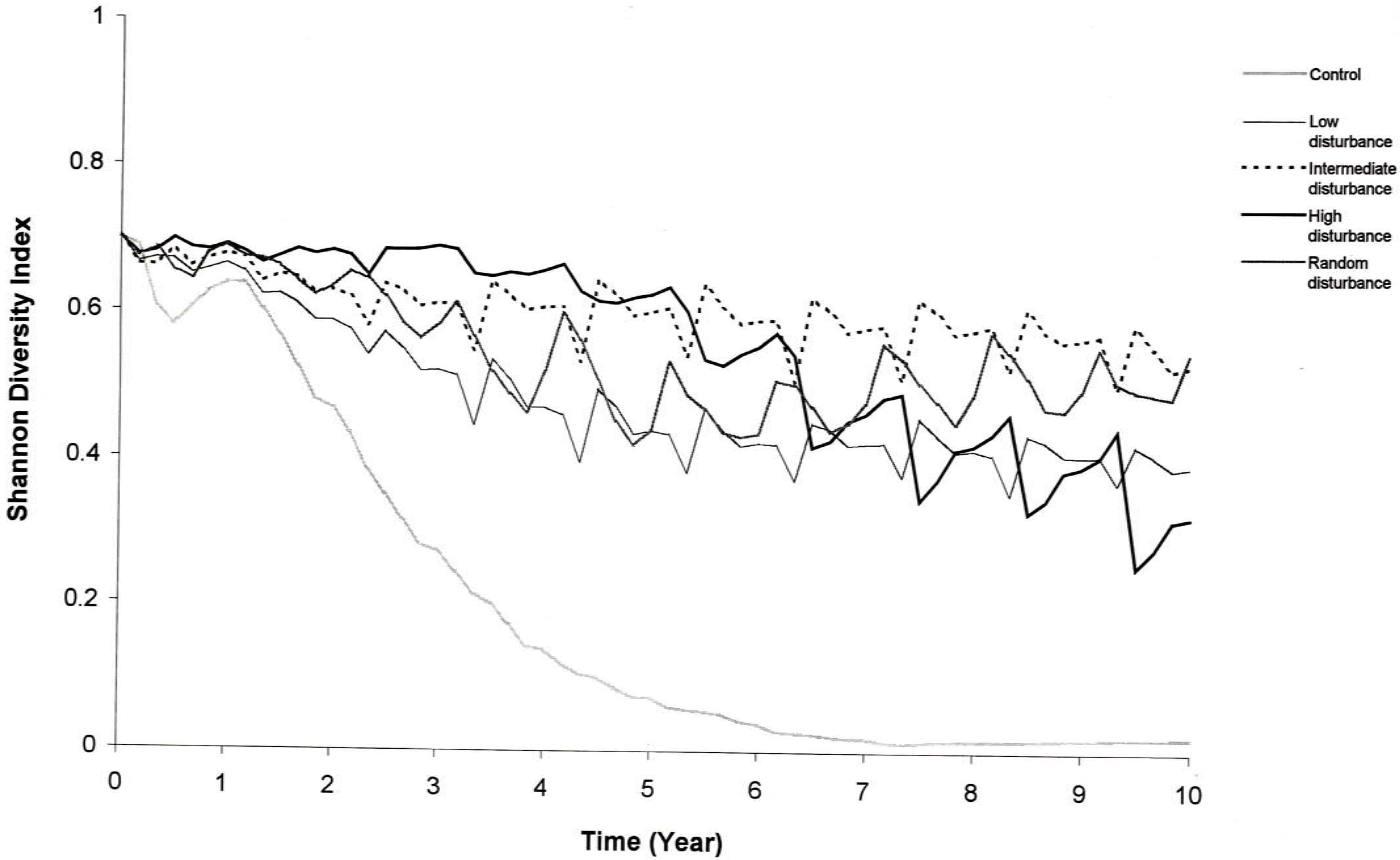
3.4.3.5 Disturbance Effect at Different Time Interval

Fixed time disturbance and random time disturbance were found to have similar effect on the dynamical behaviour of the coral community simulated (Figures 3.21 - 3.25). The trajectory and final area cover of each coral was found to be not significantly different in simulations with either fixed or random time intermediate disturbance level. Similar behaviour was also observed for the species diversity of the coral community simulated under both fixed and random time disturbance (Figure 3.26).

3.4.4 Utility of the Object-oriented Model

Object-oriented model developed in this research appears to be useful as a tool to elucidate some mechanisms structuring the diversity in a coral community. While only the effects of different degrees of disturbance, time of disturbance and temperature were considered in the simulation, it is likely that an even better and more realistic model could be developed if these factors could be fine tuned, and other parameters could be incorporated in the simulation. Verification of the modelling results should be carried out and part of this would be discussed in the following chapter.

Figure 3.26. Change of average Shannon-Wiener species diversity index in the simulation under different levels of disturbance.


Shannon Diversity Index
1
0.8
0.6
0.4
0.2
0
0
1
2
3
4
5
6
7
8
9
10
Time (Year)
Control
Low disturbance
Intermediate disturbance
High disturbance
Random disturbance

CHAPTER 4 GENERAL DISCUSSION

4.1 Mechanisms Structuring a Coral Community

As corals are sessile animals, colonization of the space for growing will be the only way for a coral to survive in a reef environment. Competing for space is undoubtedly the main goal for a coral during interspecific competition, whoever wins in the competition can survive while the one that loses will not. Biological characteristics of the corals are critical in structuring a coral community.

Based on the computer model developed (Section 3.4.2), fast-growing habit with overtopping competitive mechanism was shown to be one of the powerful strategies for a coral to gain dominance in a stable environment. Faster rate of colonization of surrounding area brought about by the fast-growing habit, no "available space" limit for radial growth and indirect killing on other corals brought about by the overtopping competitive mechanism, made the branching / tabular form corals (Group 4 corals) dominant in a stable reef environment. In nature, coral species with such biological characteristics were also usually found to be dominant in a shallow water coral community (Sorokin, 1993).

Disturbance and the biological response towards disturbance may be the main structuring factors of a coral community in an unstable reef environment. Both the disturbance-resistant characteristics of corals, indicated by their different sensitivities to disturbance, and the types of damage on corals during disturbance were found to affect coral dominance (Section 3.4.3.2). For example, under the simulated environment, the low sensitivity of foliaceous corals (Group 2 corals) towards disturbance and the type of damage sustained by them during a disturbance contributed to their becoming the dominant coral group in a reef environment with high level of disturbance. This scenario appears to be operating as well in the natural environment.

Simulation results from the computer model also indicated the ability of disturbance to maintain species diversity in a coral community. Significantly high species diversity was observed in the simulated coral community exposed to intermediate level of disturbance (Section 3.4.3.4). Hence, this computer exercise appears to be able to reveal one of the mechanisms maintaining species diversity in a complex coral community predicted by the "intermediate disturbance hypothesis" (Connell, 1978).

The importance of dominant species in structuring the coral community was also demonstrated by the model developed. The final area cover of the dominant coral group (Coral Group 4) was significantly decreased when there was disturbance (Section 3.4.3.3). The decrease in the total area cover of the dominant corals provided more space for other corals to colonize and survive in the reef environment The increase in the survival of the less dominant corals also resulted in a significant increase in the species diversity of a coral community.

Thus, in general, this object-oriented computer model developed appears to be able to depict the role of physical disturbance (e.g. hurricane) as the main structuring factor of a coral community. Different sensitivities and responses of different coral species to disturbance also led to the formation of different community structure. Such results agreed well with field observations on the effect of storm disturbance in structuring the shallow water coral communities (Porter *et al.*, 1981; Woodley *et al.*, 1981).

4.2 Comparison between Field Studies and the Computer Model

In order to compare the results from the simulation and those from field observations, corals identified from the extensive field studies in Ping Chau (Section 2.4.2.2) were re-grouped into the same five coral groups used in the computer simulation. This is done for each defined zone of the study area (Tables 4.1 and 4.2). The composition of the coral groups and the species diversity for each defined zone were then used to compare with those obtained from the computer simulations. Proportional Similarity value, *PS* value (Section 2.4.2.2), was used to compare the community similarity. As the field study area was randomly selected and initial conditions for the computer simulation were also randomly determined, Shannon-Wiener diversity index was used (Brower *et al.*, 1990) to measure the species diversity. Data generated at every one-sixth of a year from the mean results of the simulations were used to compare with those from field observations. Significance of difference in species diversity was tested by Student *t* test (Zar, 1996).

With two exceptions, indices of species diversity of the communities generated from the computer simulation do not conform to any of those calculated from the field data. Only the species diversity of two defined zones of the study area were found to be similar to that generated from the model (Table 4.3, Figures 4.1 and 4.2). The species diversity of Zone 2 was found not significantly different from that of the simulated coral community under fixed time, high level of disturbance at the time interval of 4.5 - 5.167 year. The community similarity (i.e. *PS* value) between Zone 2 and the simulated coral community at this time interval ranged from 69.68% to 73.52%. The species diversity of Zone 4 was also found not significantly different from that of the simulated coral community under fixed time intermediate level of disturbance at the time interval of 4 - 9 years. The *PS* value calculated ranged from 76.03% to 81.16%.

The similarity in the coral community structure observed between the field data (Zones 2 and 4) and that generated from the computer model resulted from the ability of the model to simulate the occurrence of the dominant coral groups found in the field. Foliaceous *Pavona decussata* (Group 2 corals) and massive form or castle-like faviids (Group 3 corals) were the two dominant coral groups found in Zone 2 (Table 4.1). These two coral groups were also identified as the two dominant groups in the computer simulated coral community under fixed time, high level of disturbance at the time interval of 4.5 - 5.167 year (Figure 4.1). As the computer model also simulated the co-existence of the rest of the other coral groups (Coral Groups 1, 4 and 5) identified in Zone 2, it follows that the coral community structure simulated coral community under fixed time, high level of disturbance at the time interval of 4.5 - 5.167 year should be similar to that found in Zone 2.

In the same token, the coral community structure observed in Zone 4 was similar to that simulated in the computer model. Branching or tabular form corals (Group 4 corals) were the dominant group found in Zone 4. This coral group was also dominant in the simulated coral community under fixed time, intermediate level of disturbance at the time interval of 4 - 9 years (Figure 4.2). As the abundance of other coral groups was also maintained in the simulated coral community under intermediate level of disturbance (Section 3.4.3.4), it is expected that the coral community structure simulated in the computer model should not be significantly different from that observed in Zone 4.

As a whole, however, the physical environment identified in Zones 2 and 4 was different from that simulated in the computer model. Based on the presence of the dominant storm-sensitive species observed in these two zones and their location in a less wave exposed and deep water environment (Section 2.4.2.2), Zones 2 and 4 were considered as stable reef environment. However, with either intermediate or high levels of disturbance, the physical environment simulated in the coral communities was unstable. Therefore, other than within the restricted time intervals, the developed model cannot completely simulate the natural coral community found in Ping Chau. There are limitations in the present computer model. Such limitations are discussed in the following section.

Table 4.1. Area cover (cm^2) and relative abundance (in parentheses) of each coral group found in the six defined zones of the study area at A Ma Wan, Ping Chau after re-grouping. For detailed description of characteristics of each zone, refer to Figure 2.5.

Coral Group No.	Corresponding Coral Groups in Nature	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6
1	Massive form *Porites lobata*	3480.44 (11.76%)	405.18 (2.08%)	2157.24 (15.&0%)	1816.87 (13.95%)	1617.64 (15.22%)	14.87 (14.87%)
2	Foliaceous *Pavona decussata*	5100.63 (17.24%)	5155.11 (26.40%)	1515.13 (11.03%)	1031.35 (7.92%)	33.33 (0.31%)	4.36 (4.36%)
3	Massive form/ Castle-like Faviids	16604.47 (56.13%)	6089.71 (31.20%)	9538.53 (69.42%)	5286.75 (40.60%)	7329.96 (68.99%)	29.90 (29.90%)
4	Branching/Tabular form Acroporids	3258.41 (11.01%)	3283.16 (16.82%)	336.93 (2.45%)	4389.27 (33.71%)	0.00 (0.00%)	2.70 (2.70%)
5	Mushroom-like *Goniopora* or *Alveopora*	1141.74 (3.86%)	4586.76 (23.50%)	191.60 (1.40%)	497.05 (3.82%)	1645.35 (15.48%)	48.18 (48.17%)

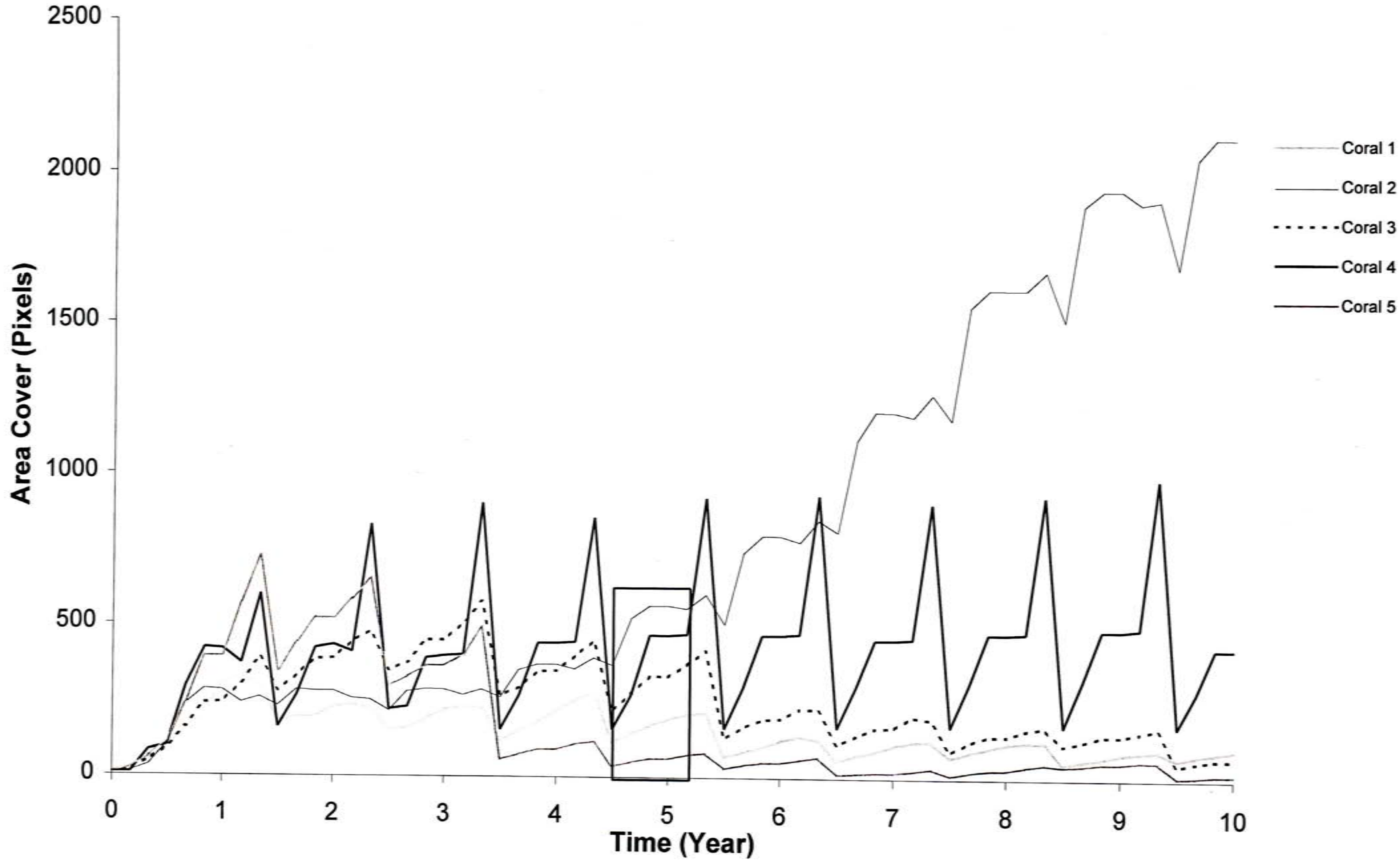
Table 4.2. Shannon-Wiener diversity index of the coral community found in the six defined zones of the study area at A Ma Wan, Ping Chau after re-grouping. For detailed description of characteristics of each zone, refer to Figure 2.5.

Zone Number	Zone Description	Shannon-Wiener Diversity Index
1	Left shallow rocky zone	0.5418
2	Left deep sandy zone	0.6235
3	Middle shallow sandy zone	0.4072
4	Middle deep sandy zone	0.5788
5	Right shallow rocky zone	0.3690
6	Right deep sandy zone	0.5343

Table 4.3. Comparison between coral community structure of Zone 2 and Zone 4 of the study area at A Ma Wan, Ping Chau and that from the mean results of the computer simulations under different levels of disturbance (only those time intervals with similar Shannon-Wiener diversity index are listed). For detailed description of characteristics of each zone, refer to Figure 2.5.

Zone Number	Disturbance Level of the Simulation	Time Interval (Year)	Range of Shannon Diversity Index in the Simulation	Community Similarity (%)
2	High	4.5 - 5.17	0.306 - 0.6090	69.68 - 73.52
4	Intermediate	4 - 9	0.5017 - 0.6402	76.03 - 81.16

Figure 4.1. Average change of total area cover of each coral group in the simulation under fixed time high level of disturbance (50% of area being disturbed each time). The time interval at which the species diversity of the simulated community was found to be not significantly different from that of the natural coral community found in Zone 2 (left deep sandy zone) is enclosed by the box .



Area Cover (Pixels)
2500
2000
1500
1000
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0
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3
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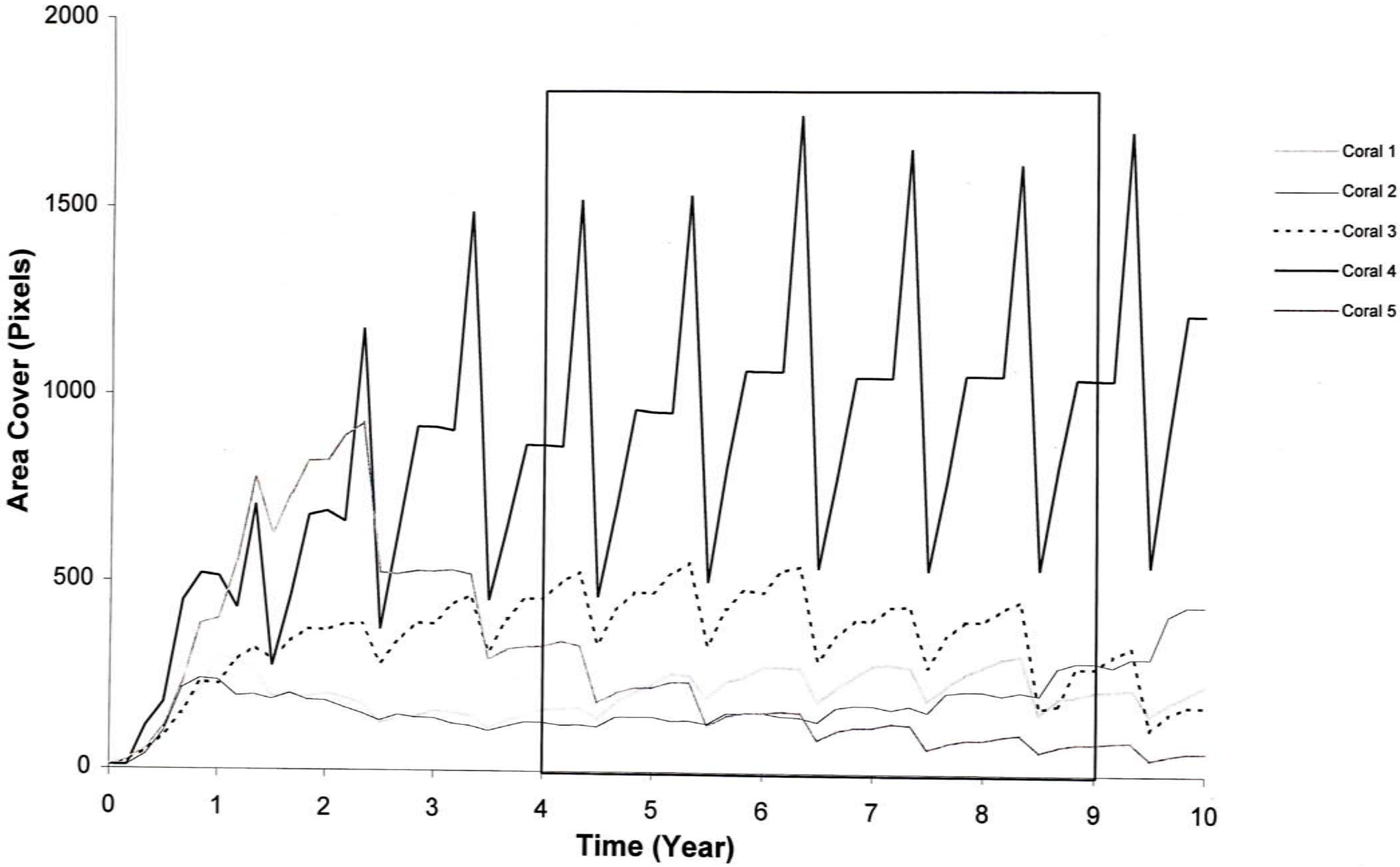
6
7
8
9
10
Time (Year)
Coral 1
Coral 2
Coral 3
Coral 4
Coral 5

Figure 4.2. Average change of total area cover of each coral group in the simulation under fixed time intermediate level of disturbance (25% of area being disturbed each time). The time interval at which the species diversity of the simulated community was found to be not significantly different from that of the natural coral community found in Zone 4 (middle deep sandy zone) is enclosed by the box .



Area Cover (Pixels)
2000
1500
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500
0
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9
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Time (Year)
Coral 1
Coral 2
Coral 3
Coral 4
Coral 5

4.3. Utilities and Limitations of the Present Model

The present work represents an initial attempt of using object-oriented approach to develop a model that would simulate the dynamics of a reef community. At this present stage of model development, many limitations to the model are to be expected.

The community structure of only two out of the six defined zones of coral community in Ping Chau was significantly similar to that simulated in the computer model. The results obtained indicated that the present ecological model developed has not been very successful in simulating the natural coral community. There could be several reasons for this. The model developed did not account for the species-specific biological characteristics of the dominant species identified in the study area. Particularly, *Platygyra sinensis* of Family Faviidae was one of the five dominant species (Figure 2.12) in each defined zone and was the most abundant species in the study area. *Platygyra sinensis* is a castle-like coral. However, no specific information is available to understand the response of this coral towards physical disturbance (e.g. hurricane). It was assumed that the behaviour of this species was similar to that of other massive form corals. In the same token, the sensitivity and the response of those corals with extending polyps, e.g. *Goniopora* or *Alveopora,* (Group 5 corals) to physical disturbance are not completely understood. The extent to which this group of corals is being damaged during hurricane is also not known. However, corals with elongated polyps were also one of the five dominant groups of corals identified in the study area. As the response and sensitivity of corals towards disturbance are important in structuring a coral community, the failure of the present computer model to incorporate the specific behaviour of groups of corals towards physical disturbance undoubtedly reduces the ability of the model to reflect the field data.

Furthermore, the physical conditions, types, degree and frequency of physical disturbance in the study area were not known. As shallow water coral community is known to be sensitive to physical disturbance (Porter *et al*, 1981; Woodley *et al.* 1981), including the actual physical conditions and information on the types and degree of disturbance occurring in the study area is necessary to increase the reliability of the model developed.

The present model also did not include the effect of other biological activities, e.g. predation and interaction with other kinds of organisms (e.g. seaweed), on the coral community. The interaction between corals and other reef organisms was also known to be important in affecting the coral community structure (Sammarco, 1980; Coyer *et al.*, 1993; Tanner, 1995). The absence of interacting effects from other reef organisms on the coral community simulated contributed an important limitation to the reliability of the present model.

Despite all these limitations, the computer model developed so far could still provide some insights on the dynamical behaviour of the natural coral community. A dominant competitive mechanism (overtopping) and fast-growing habit are successful strategies for a coral to gain dominance in a stable reef environment. Disturbance and biological responses towards disturbance are also important in structuring the disturbance-sensitive coral community. High species diversity in a coral community is maintained under intermediate level of disturbance.

The history of a coral community was identified as one of the factors influencing the dynamics of that community (Hughes, 1989). Since extensive survey has only been done in the study area for one time, and there was no previous record on the coral community studied, continuous survey on a regular basis should provide more information on the dynamical change in this coral community. As Zones 2 and 4 of the study area were significantly similar only to the simulated community at certain time intervals under high and intermediate levels of disturbance respectively (Figures 4.1 and 4.2), once additional information becomes available, further comparison could be made to verify if the dynamical behaviour of the different zones of the natural coral community would follow the one projected from the computer simulation.

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APPENDIX

A1-A5	Change of area cover of each coral group in each simulation without disturbance.
A6-A10	Change of area cover of each coral group in each simulation under fixed time low level of disturbance (10% area being disturbed each time).
A11-A15	Change of area cover of each coral group in each simulation under fixed time intermediate level of disturbance (25% area being disturbed each time).
A16-A20	Change of area cover of each coral group in each simulation under fixed time high level of disturbance (50% area being disturbed each time).
A21-A25	Change of area cover of each coral group in each simulation under random time intermediate level of disturbance (25% area being disturbed each time).

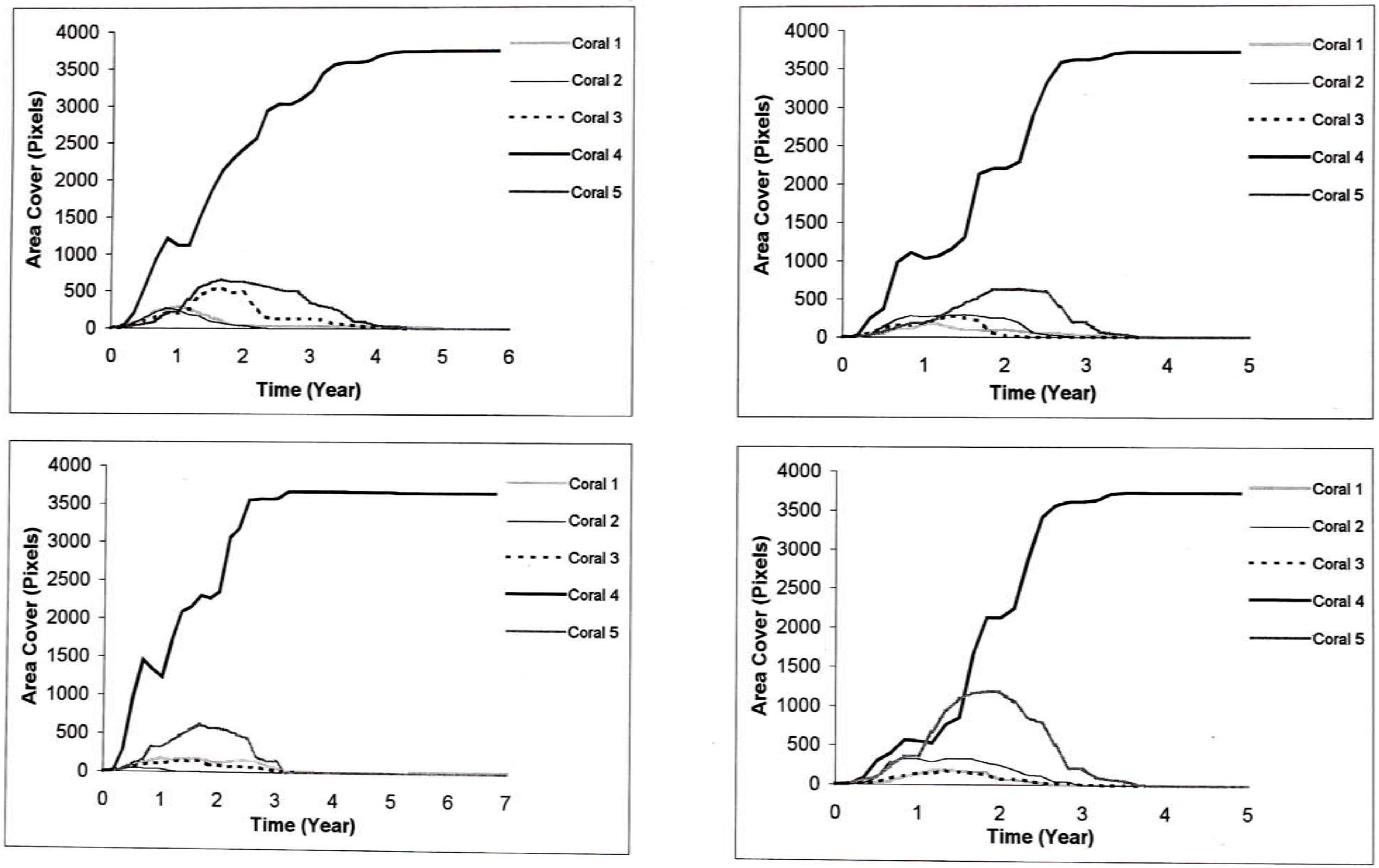


Figure A1. Change of area cover of each coral group in each simulation without disturbance.

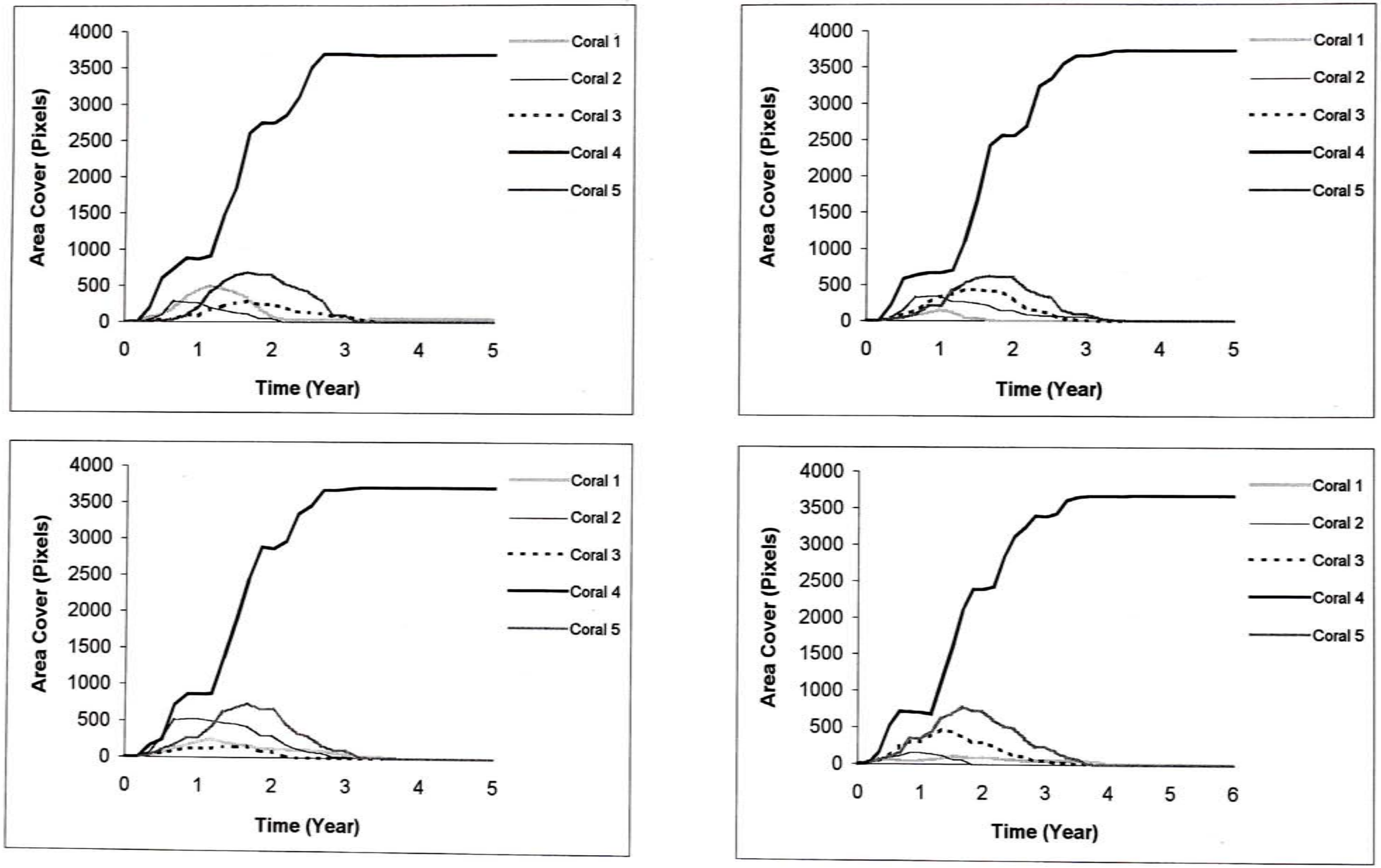


Figure A2. Change of area cover of each coral group in each simulation without disturbance.

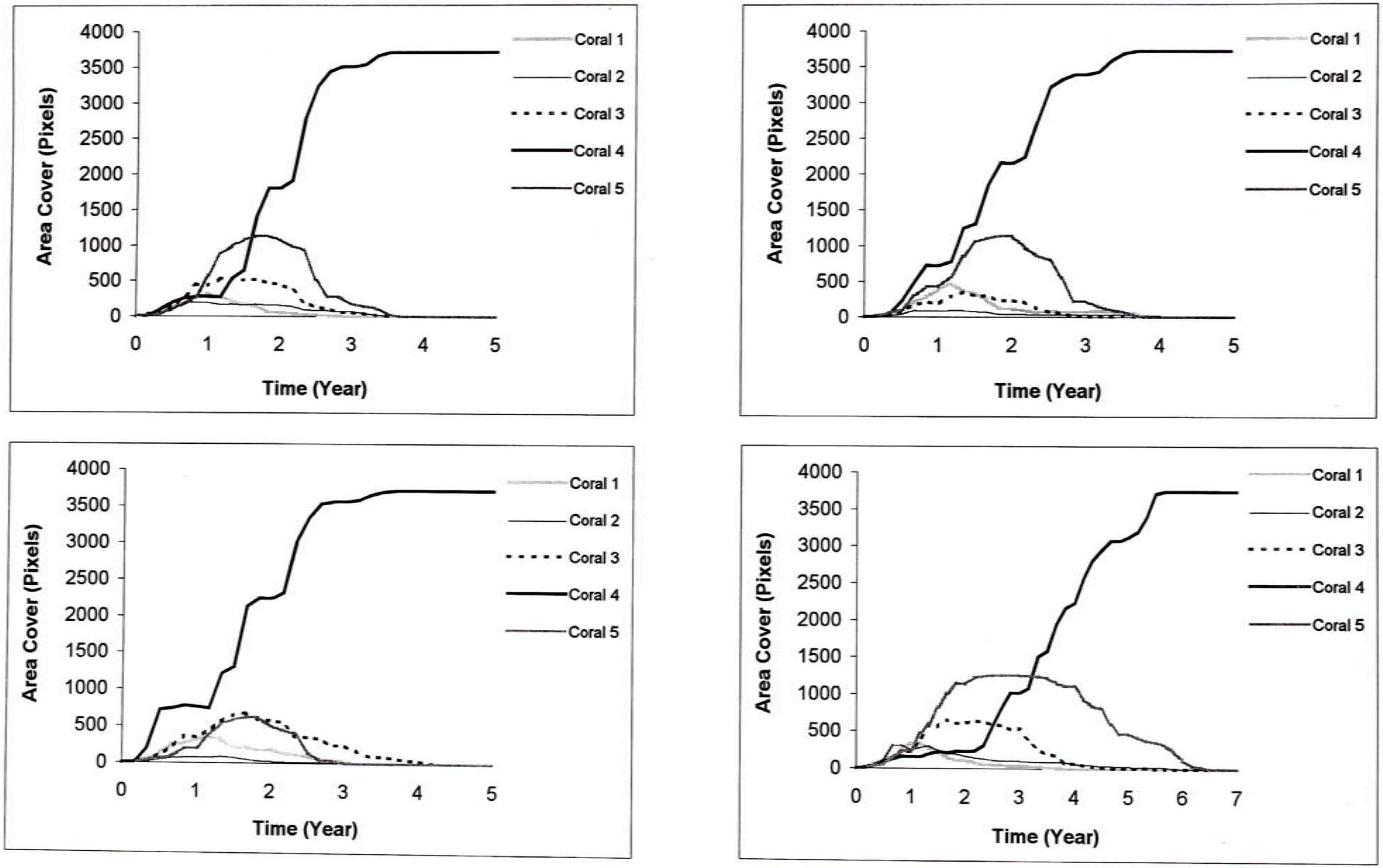


Figure A3. Change of area cover of each coral group in each simulation without disturbance.

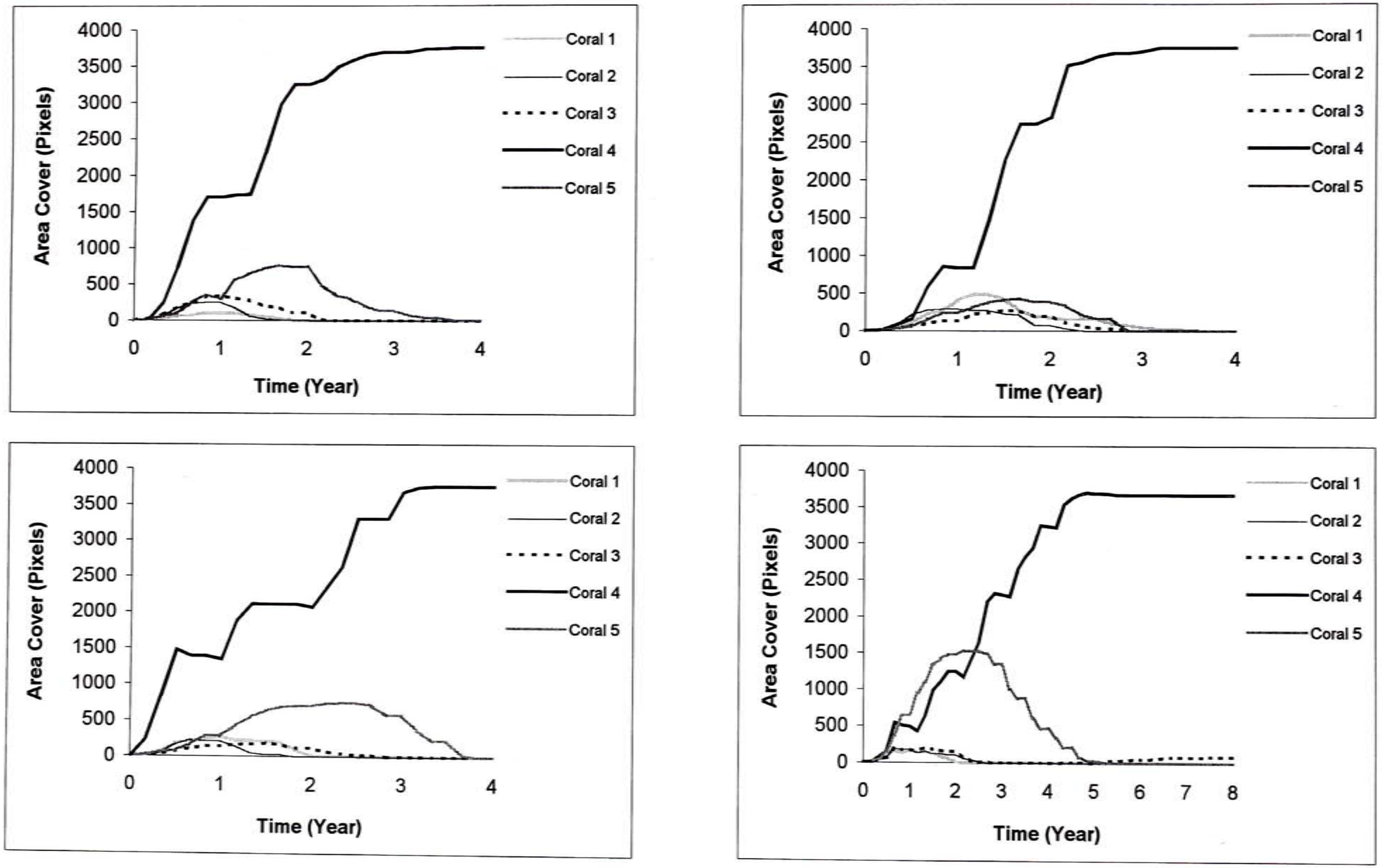


Figure A4. Change of area cover of each coral group in each simulation without disturbance.

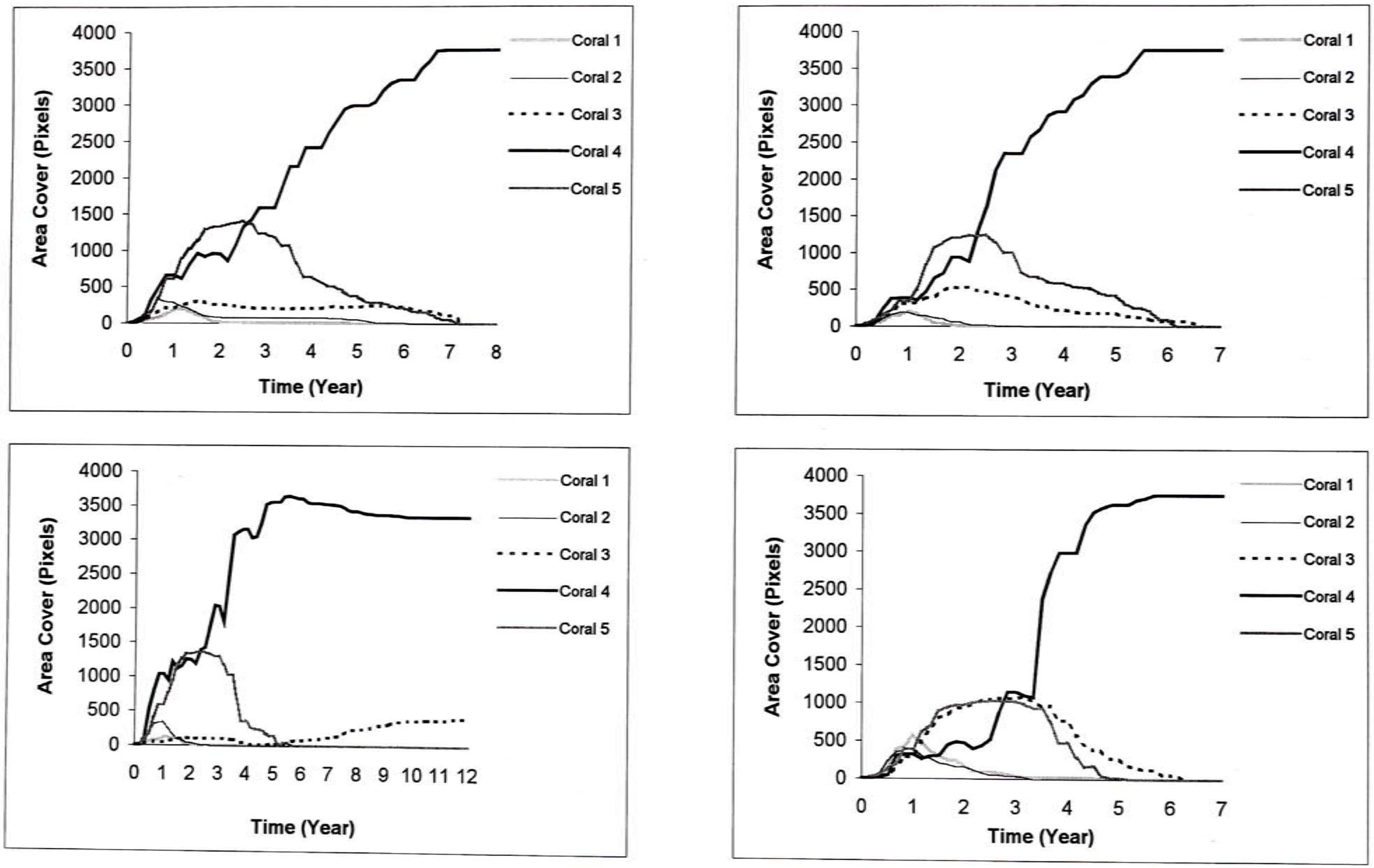


Figure A5. Change of area cover of each coral group in each simulation without disturbance.

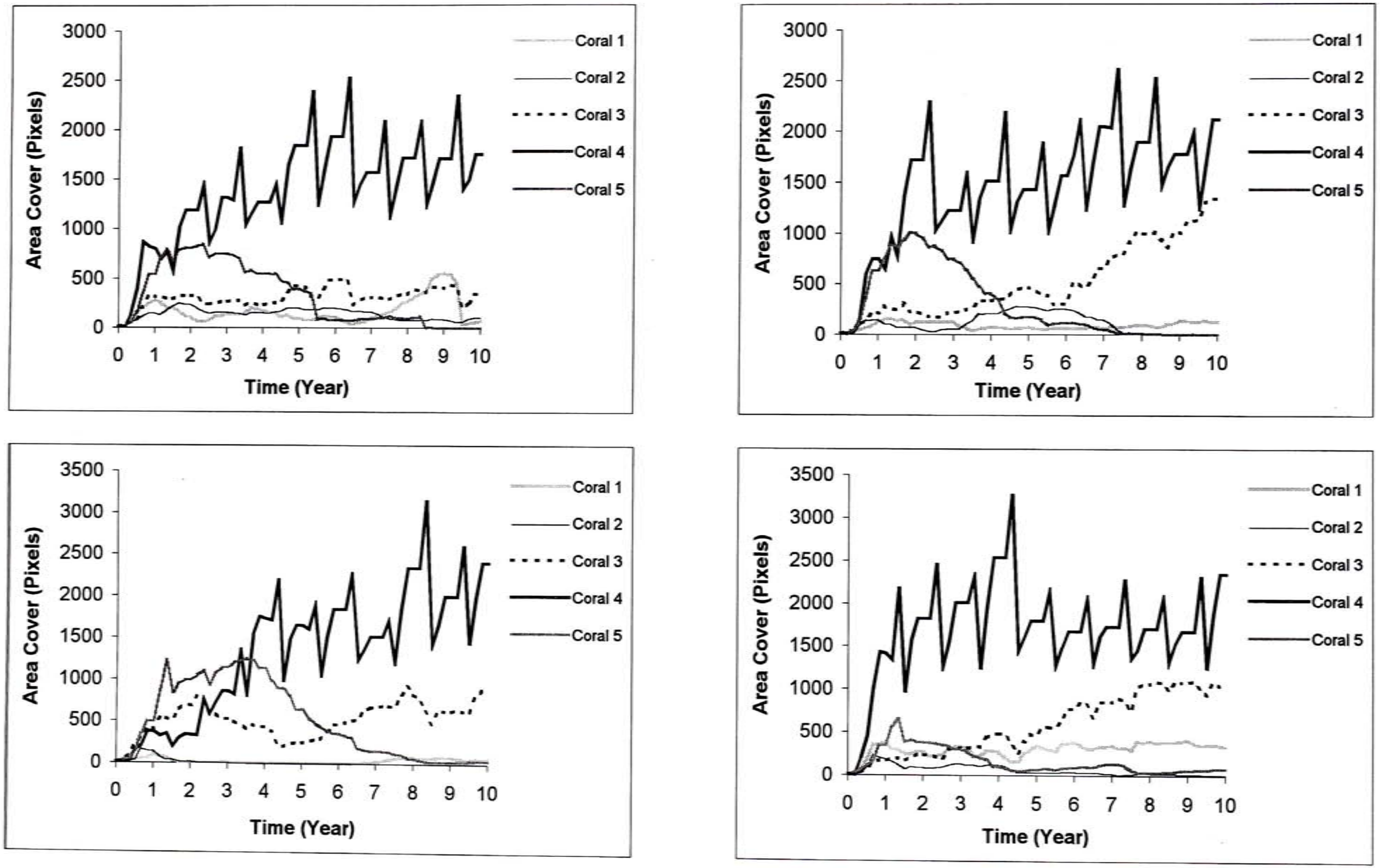


Figure A6. Change of area cover of each coral group in each simulation under fixed time low level of disturbance (10% area being disturbed each time).

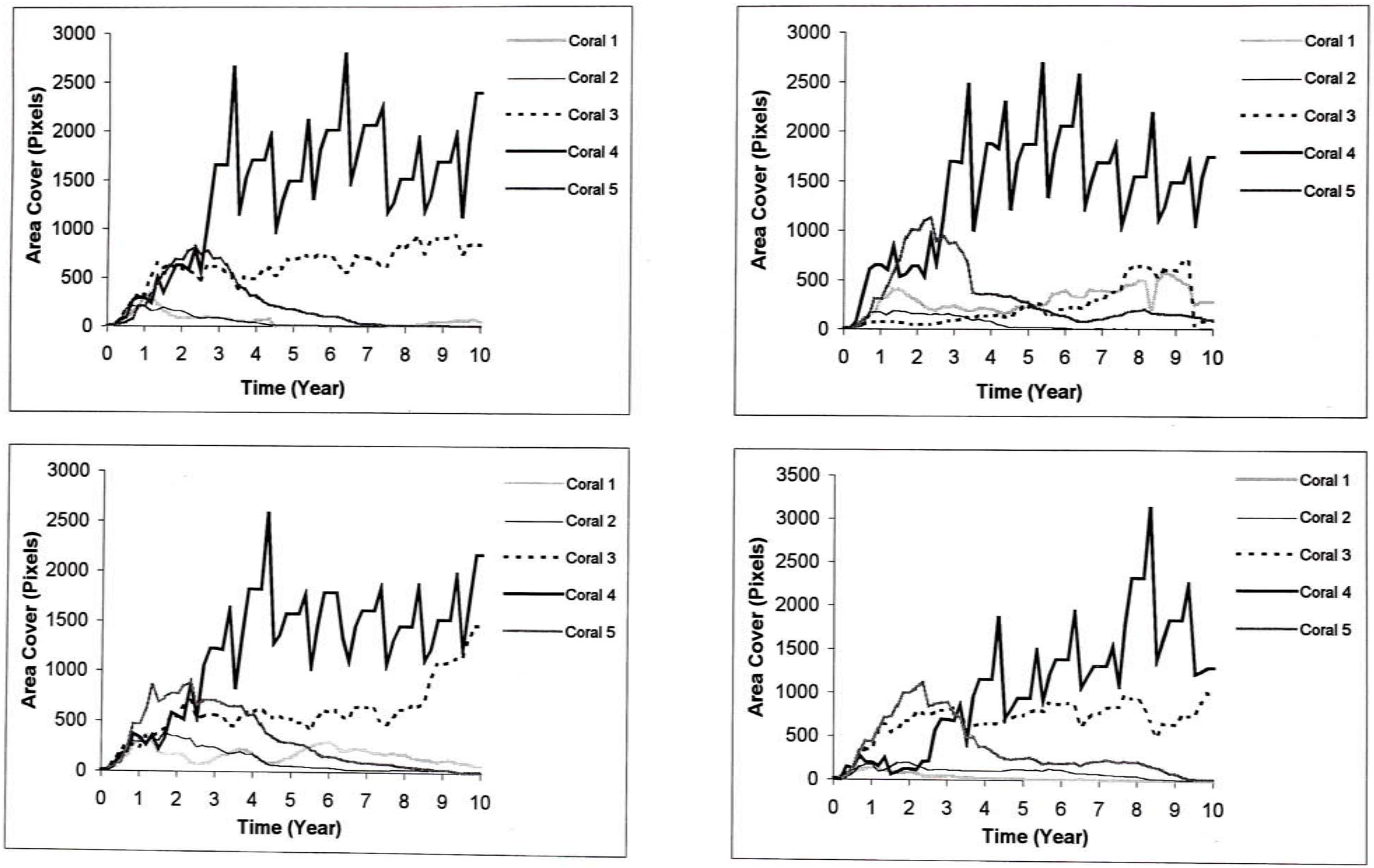


Figure A7. Change of area cover of each coral group in each simulation under fixed time low level of disturbance (10% area being disturbed each time).

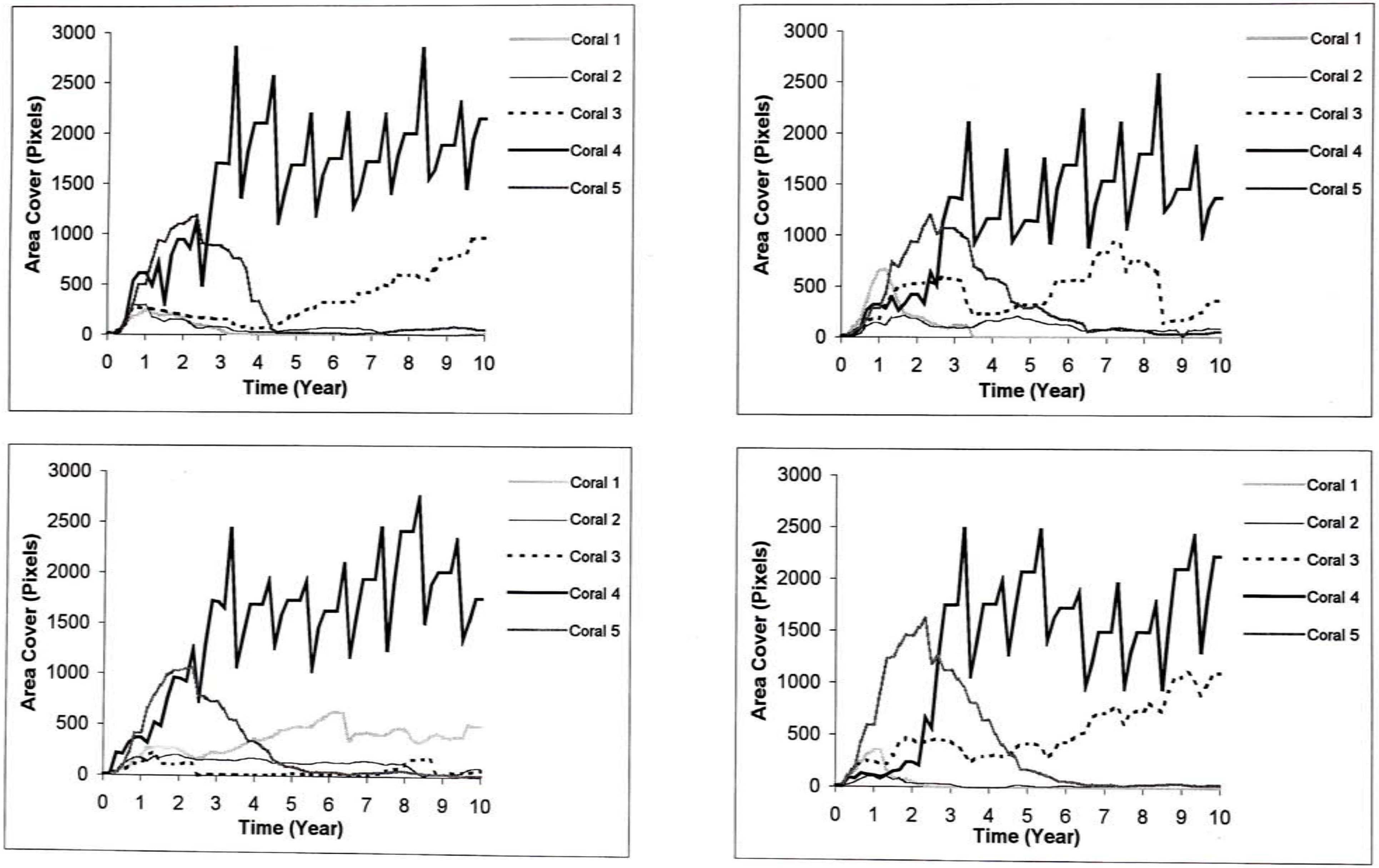


Figure A8. Change of area cover of each coral group in each simulation under fixed time low level of disturbance (10% area being disturbed each time).

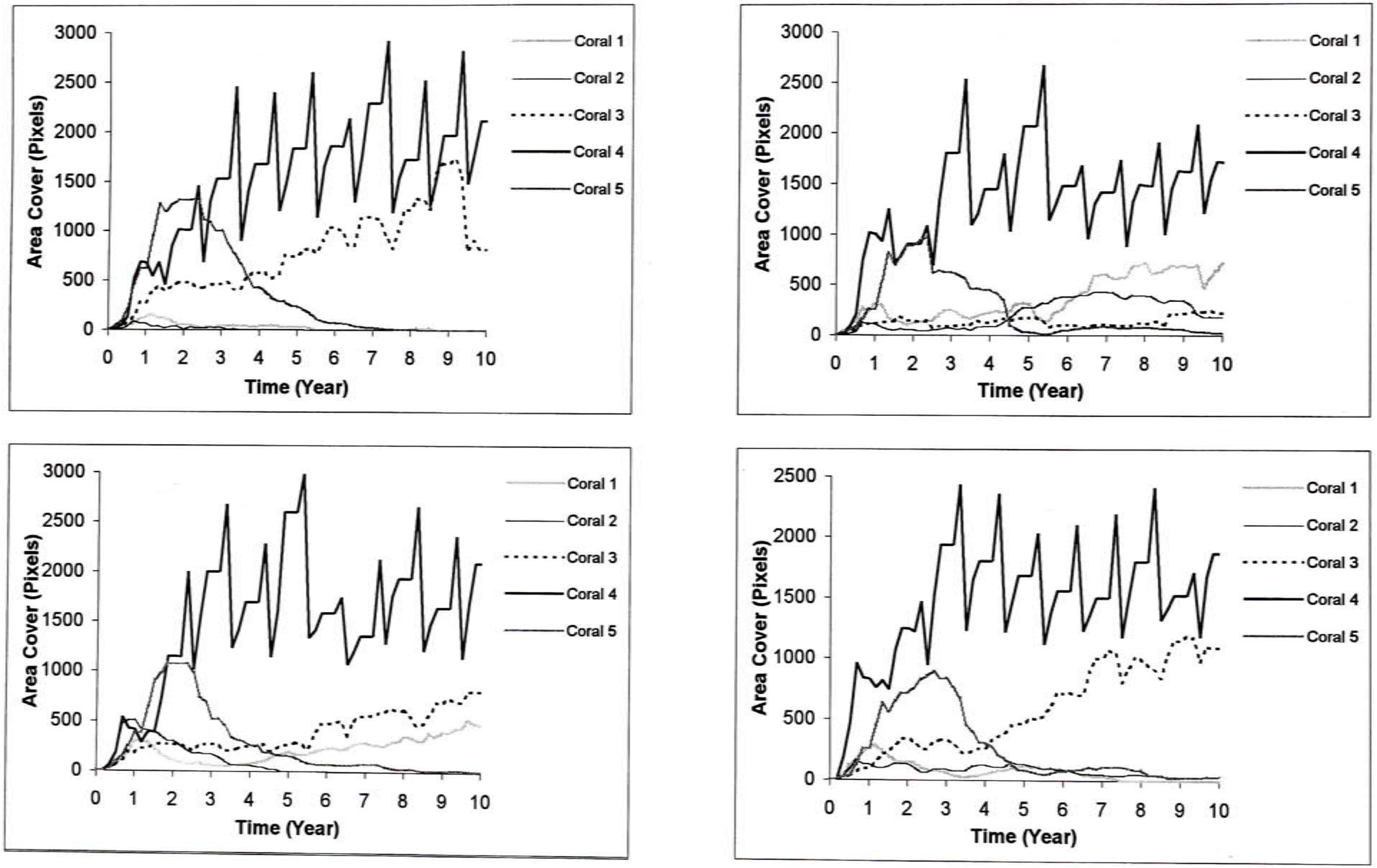


Figure A9. Change of area cover of each coral group in each simulation under fixed time low level of disturbance (10% area being disturbed each time).

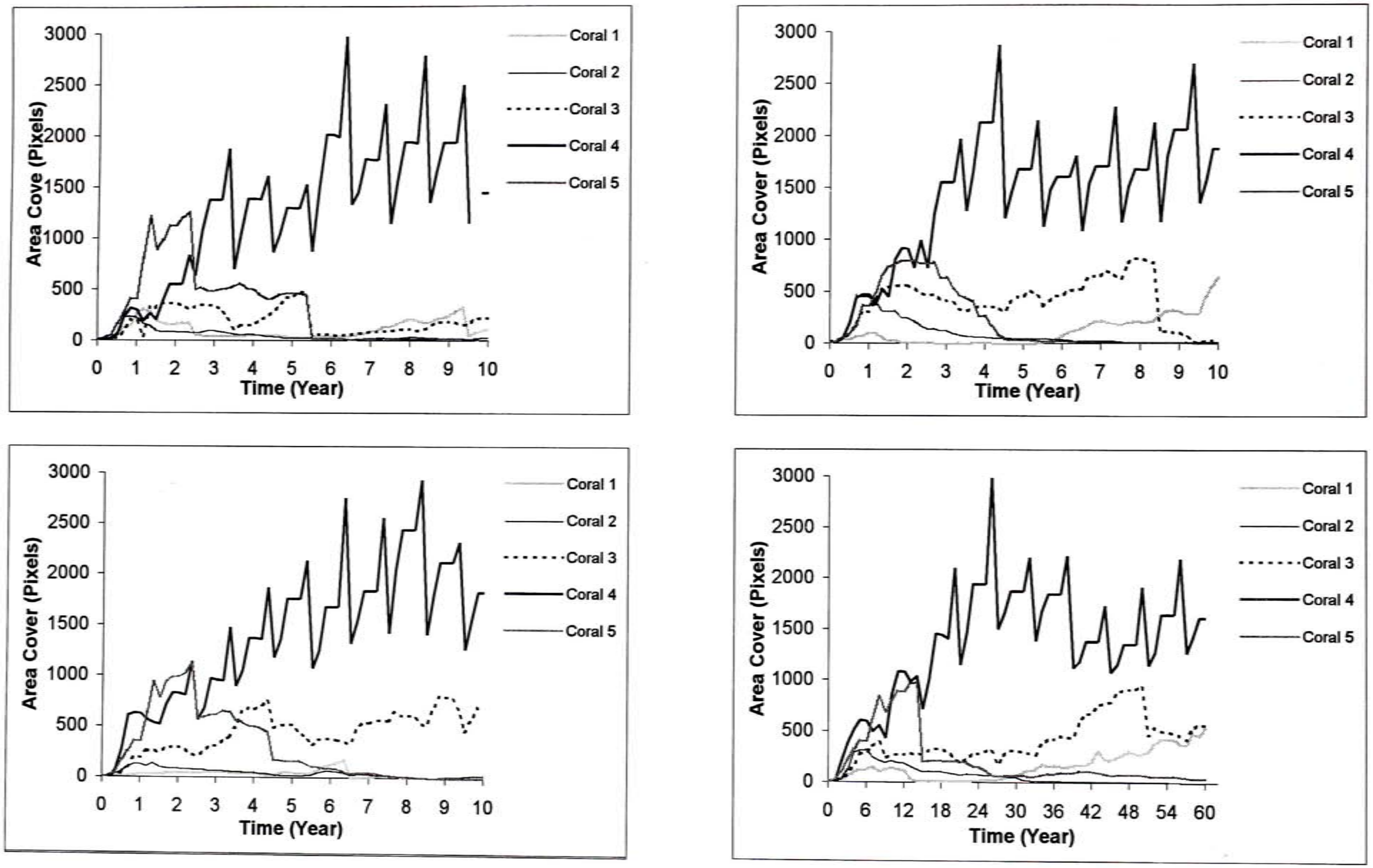


Figure A10. Change of area cover of each coral group in each simulation under fixed time low level of disturbance (10% area being disturbed each time).

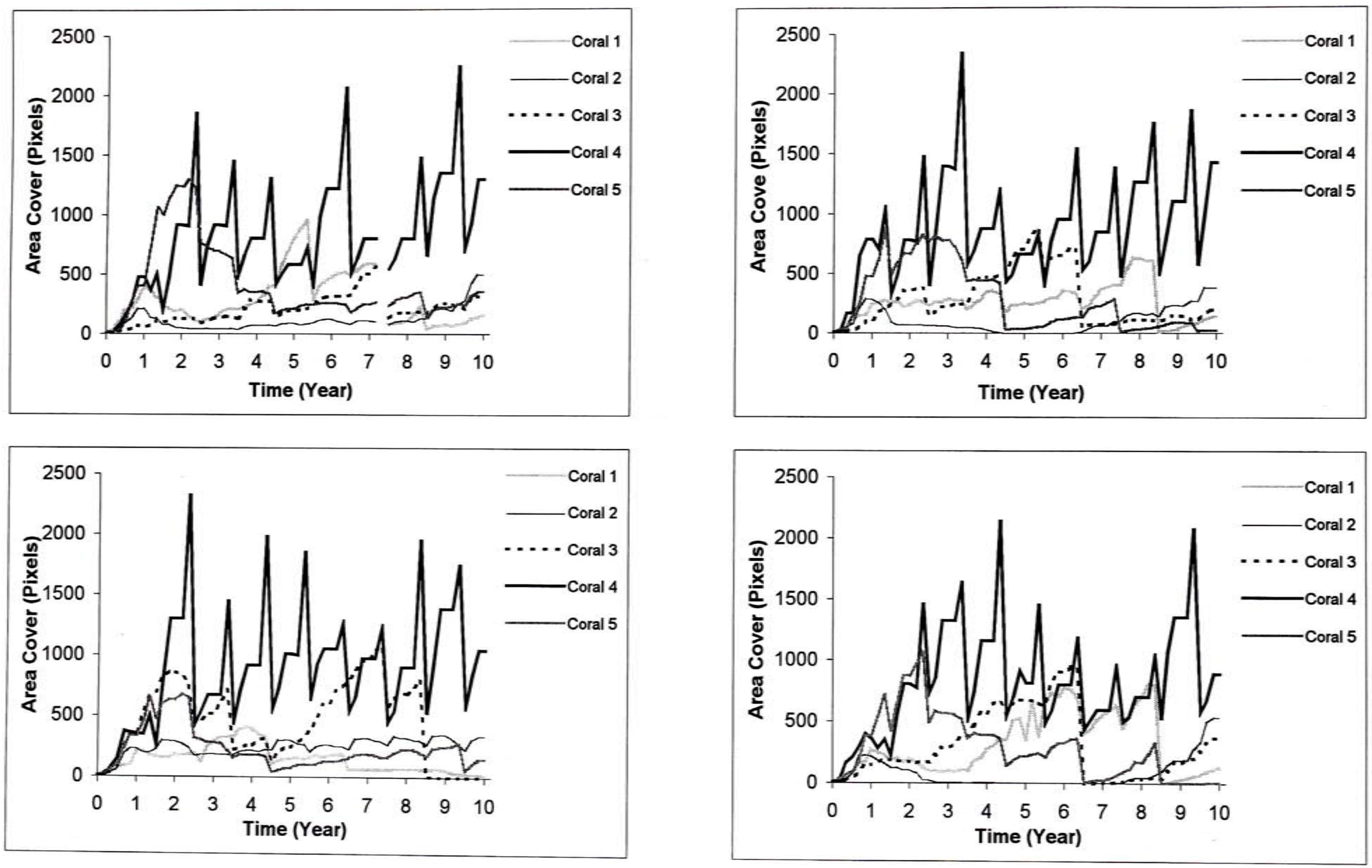


Figure A11. Change of area cover of each coral group in each simulation under fixed time intermediate level of disturbance (25% area being disturbed each time).

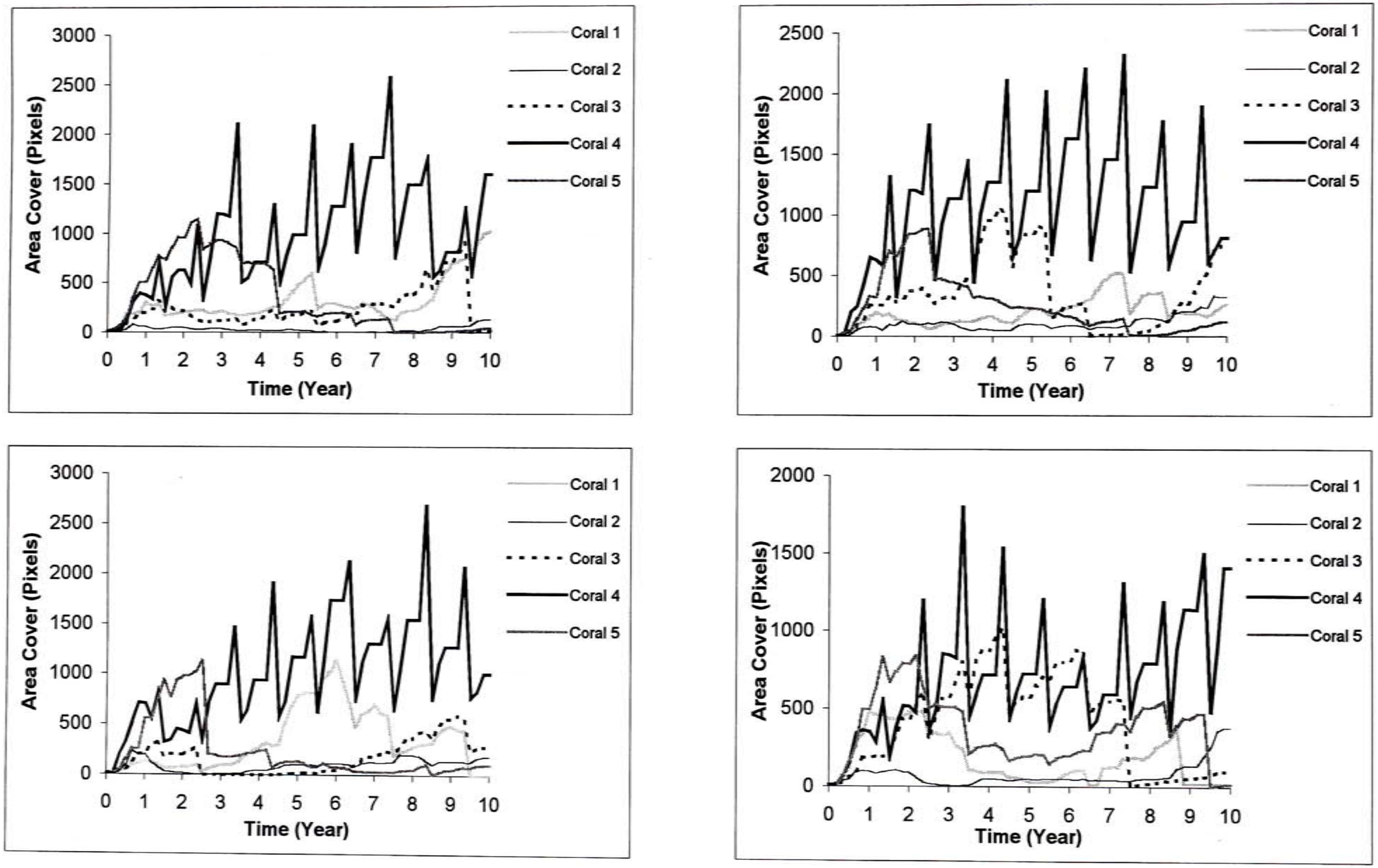


Figure A12. Change of area cover of each coral group in each simulation under fixed time intermediate level of disturbance (25% area being disturbed each time).

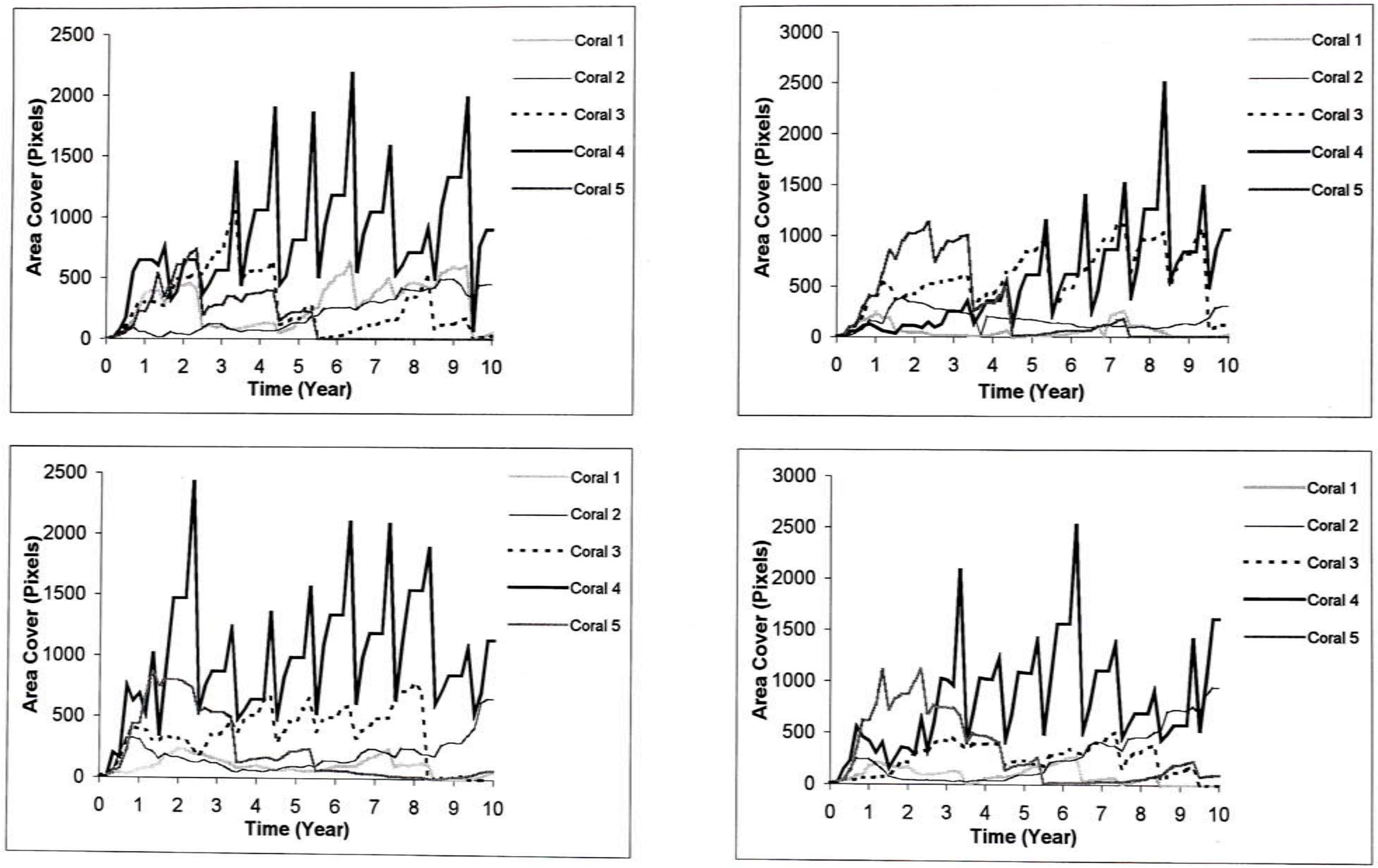


Figure A13. Change of area cover of each coral group in each simulation under fixed time intermediate level of disturbance (25% area being disturbed each time).

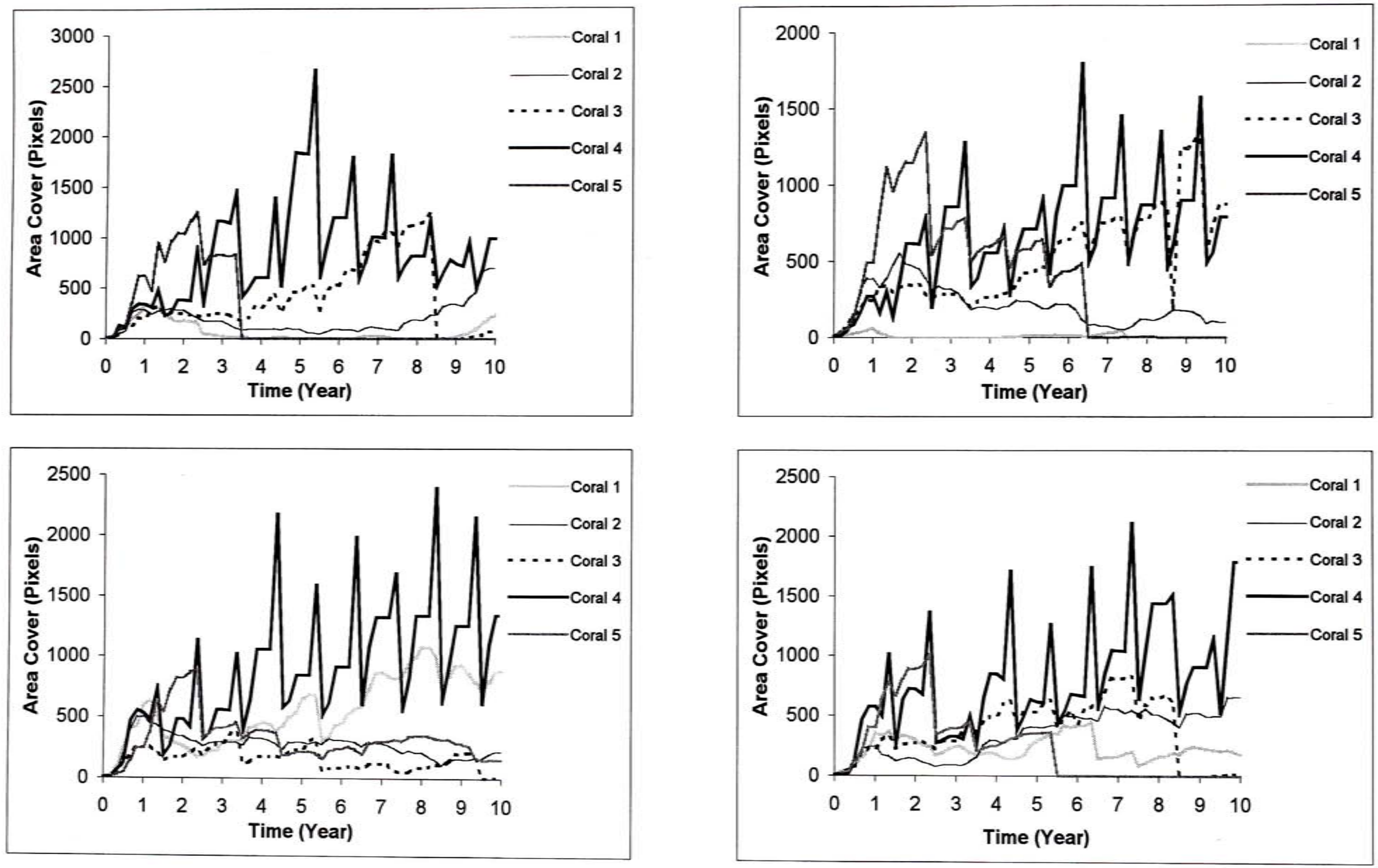


Figure A14. Change of area cover of each coral group in each simulation under fixed time intermediate level of disturbance (25% area being disturbed each time).

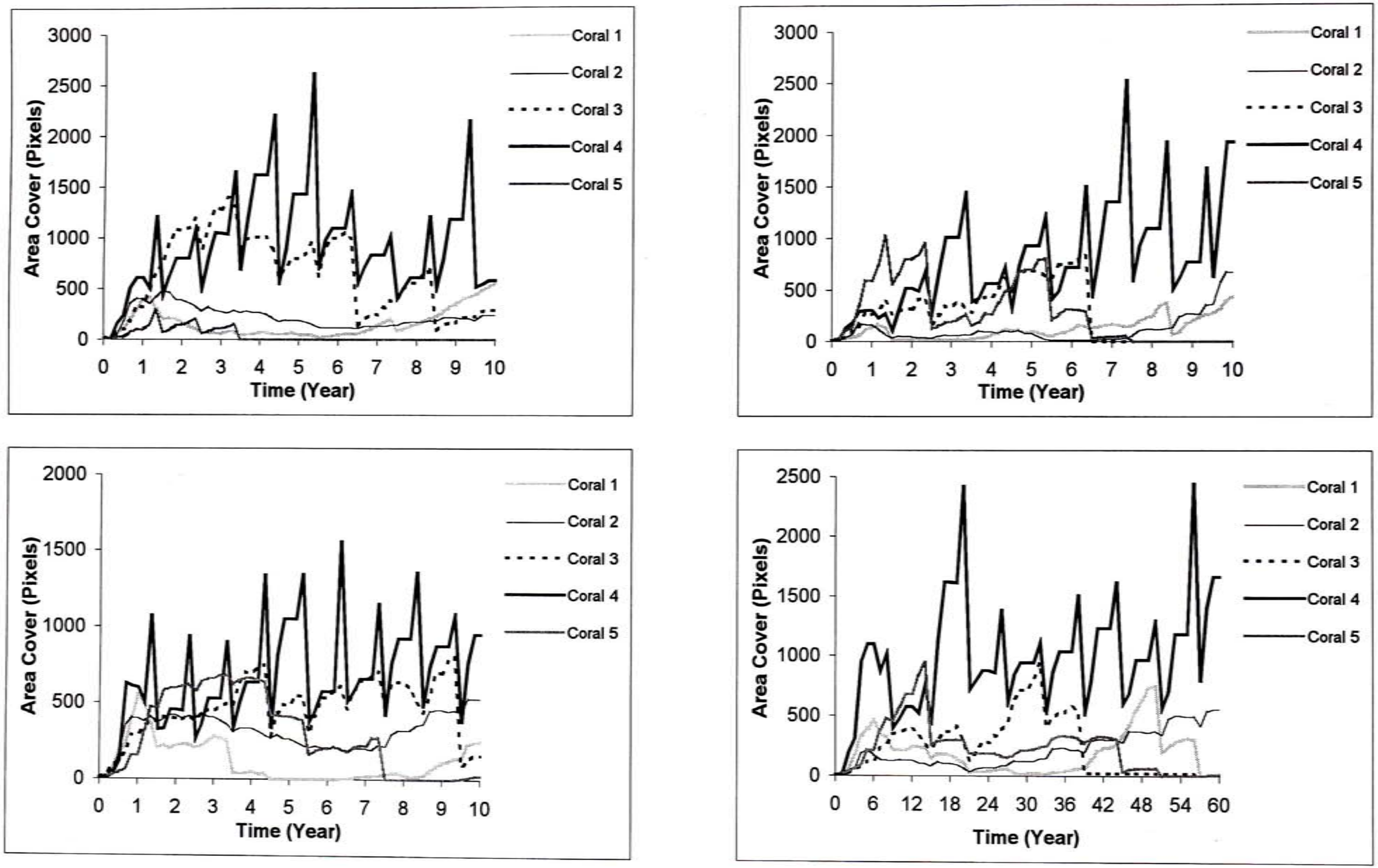


Figure A15. Change of area cover of each coral group in each simulation under fixed time intermediate level of disturbance (25% area being disturbed each time).

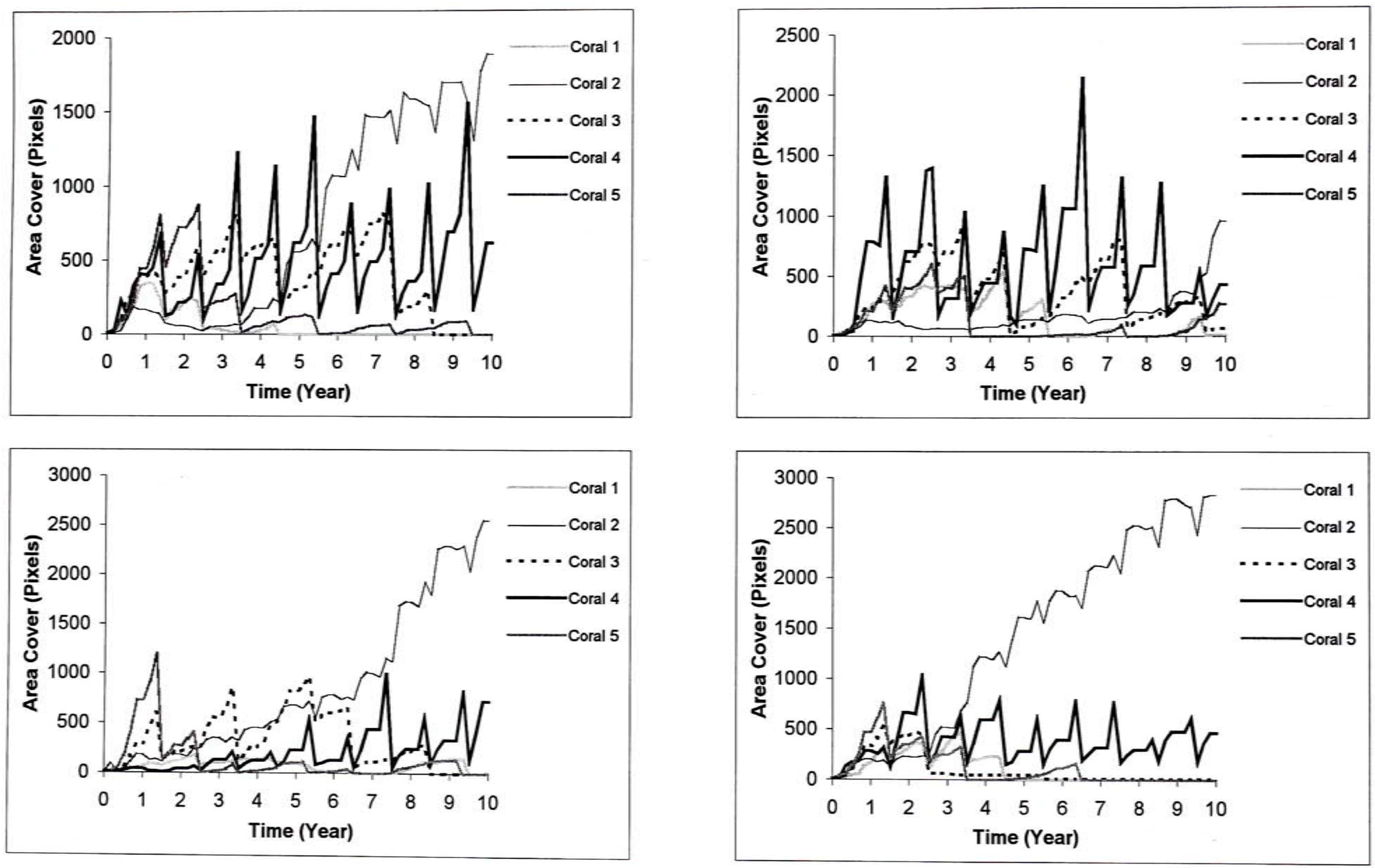


Figure A16. Change of area cover of each coral group in each simulation under fixed time high level of disturbance (50% area being disturbed each time).

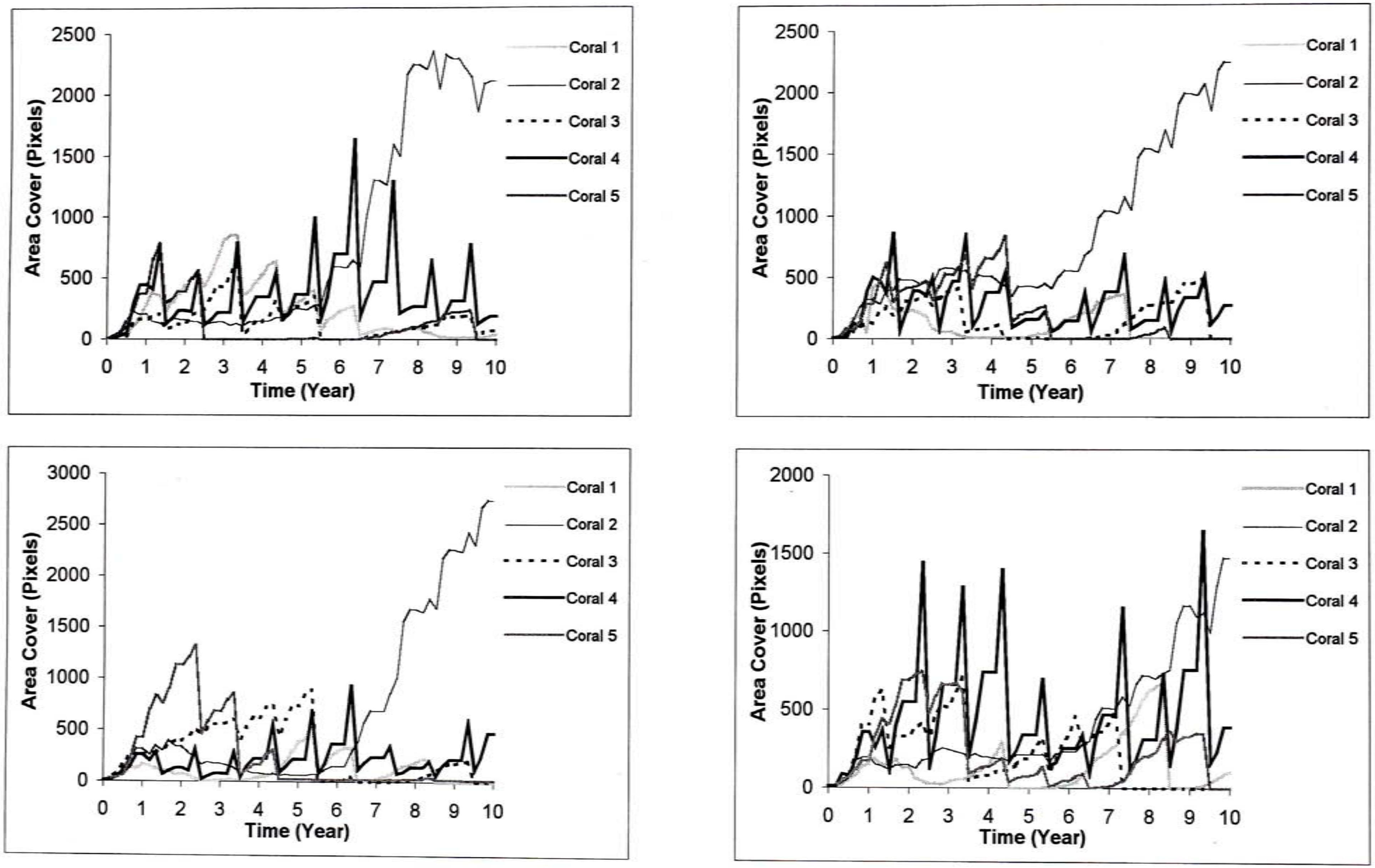


Figure A17. Change of area cover of each coral group in each simulation under fixed time high level of disturbance (50% area being disturbed each time).

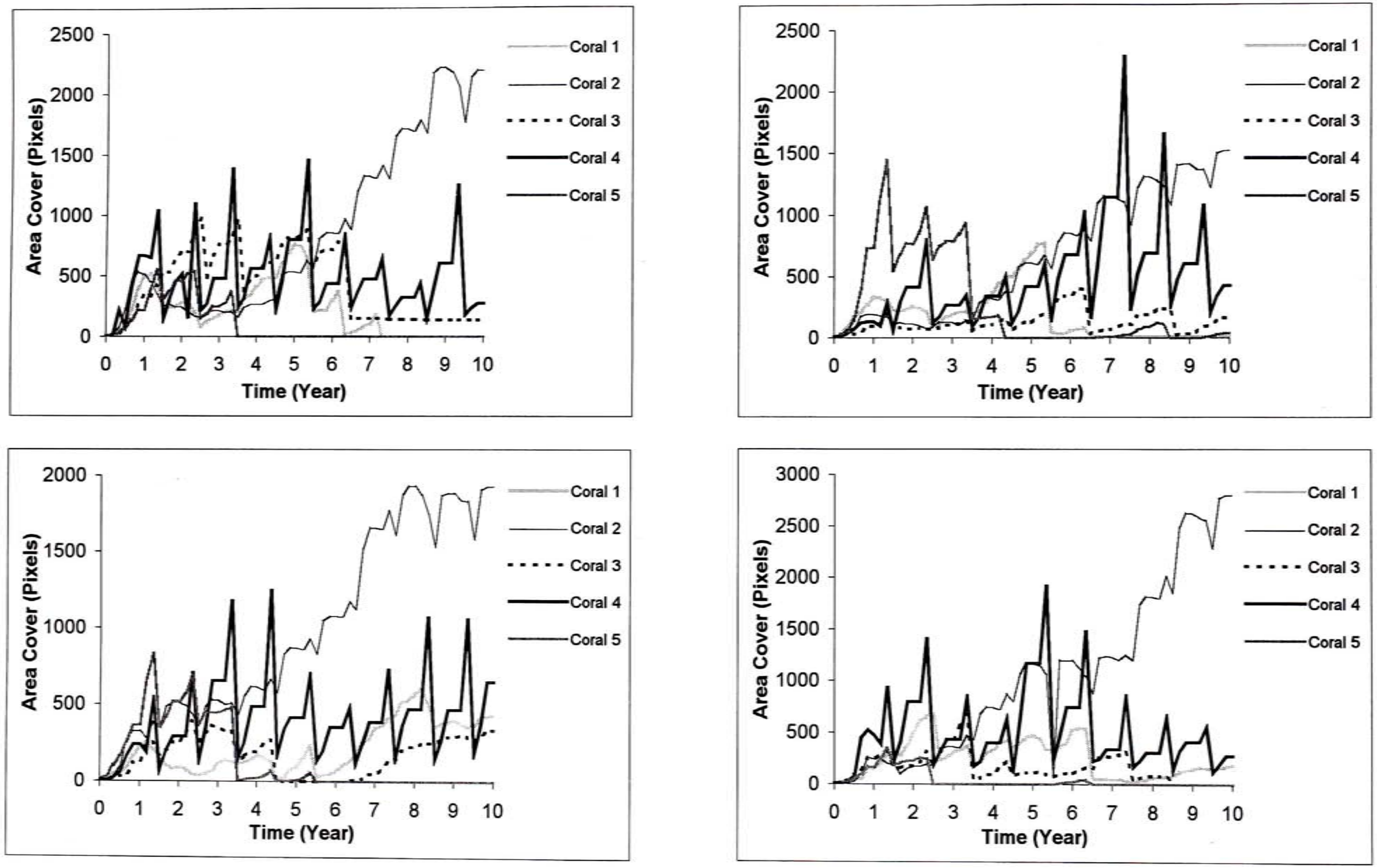


Figure A18. Change of area cover of each coral group in each simulation under fixed time high level of disturbance (50% area being disturbed each time).

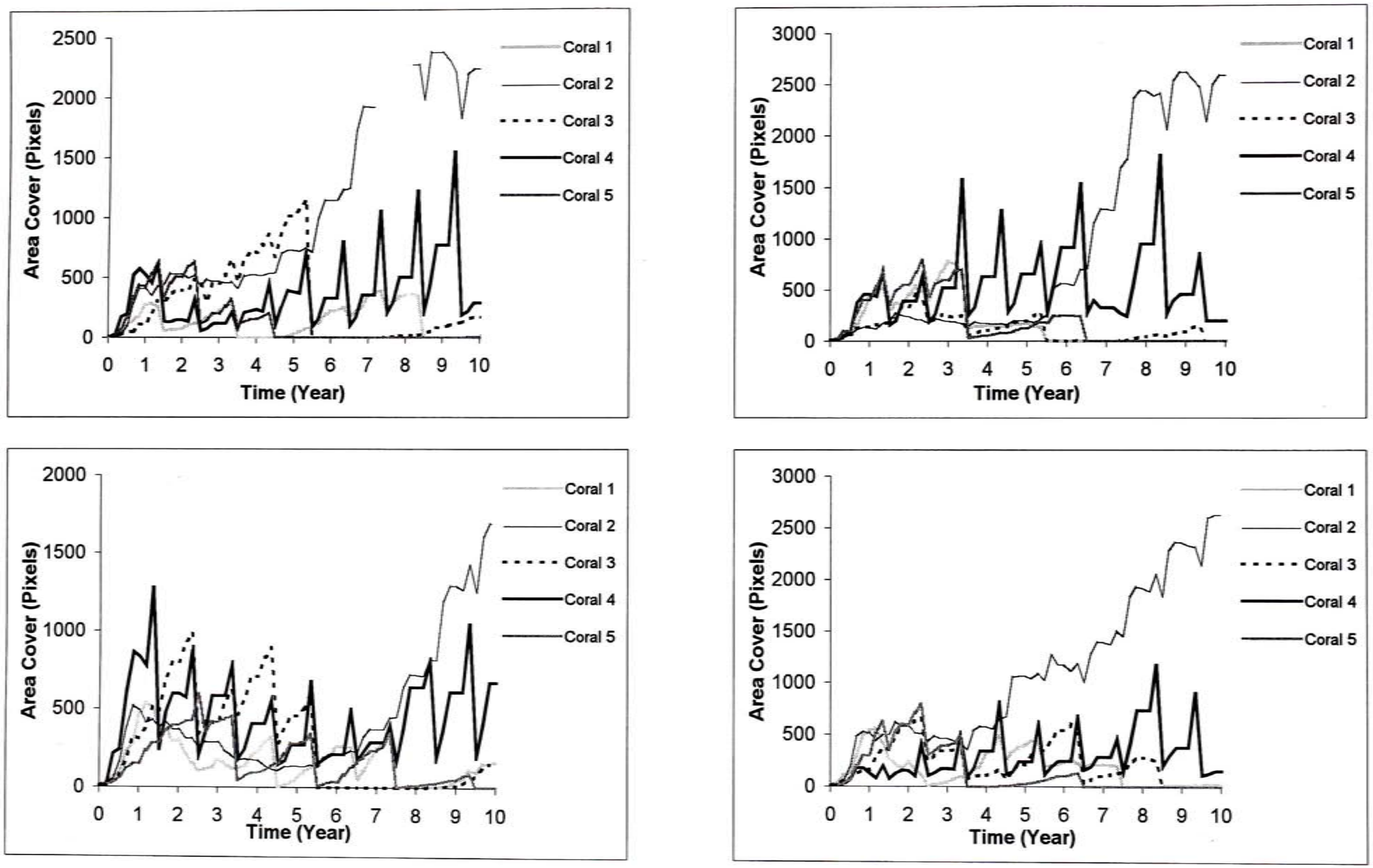


Figure A19. Change of area cover of each coral group in each simulation under fixed time high level of disturbance (50% area being disturbed each time).

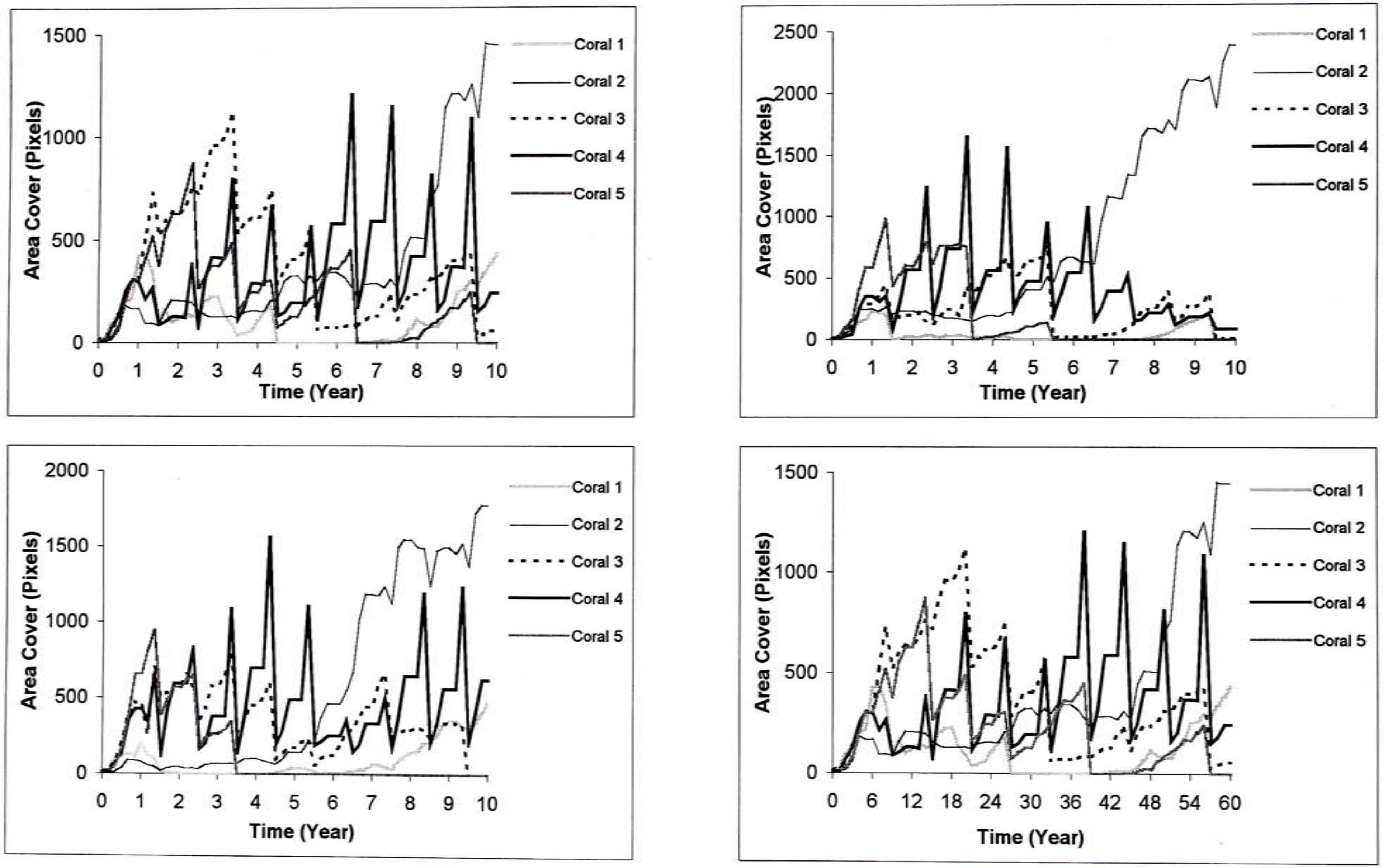
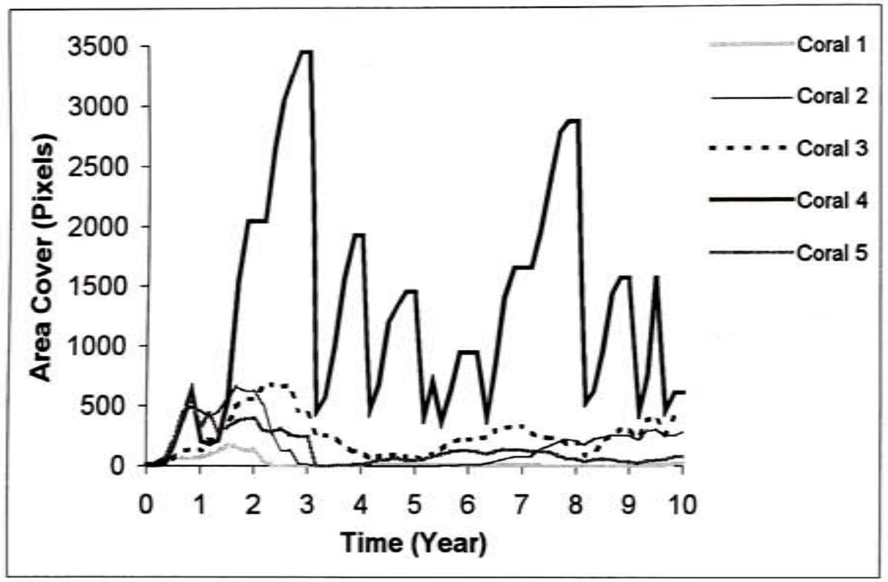
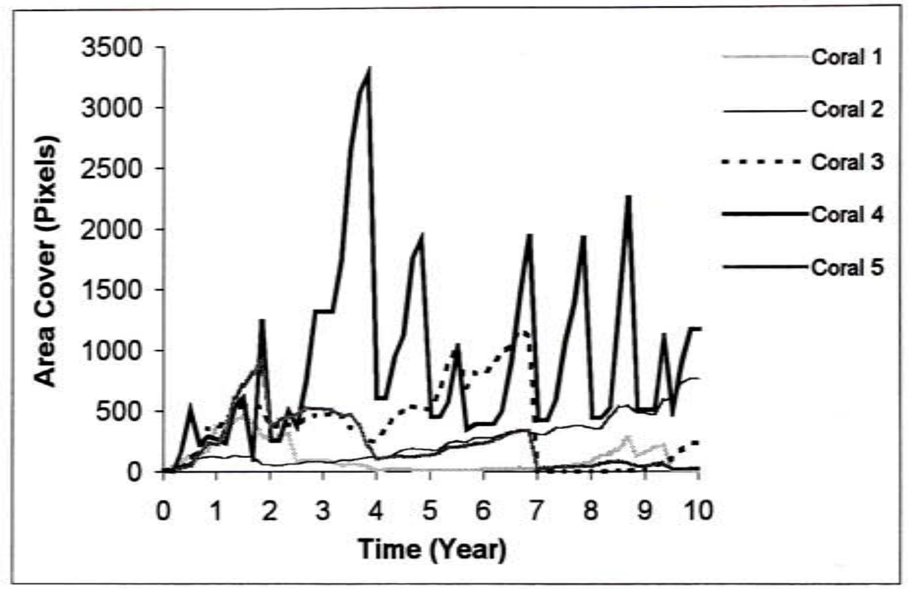
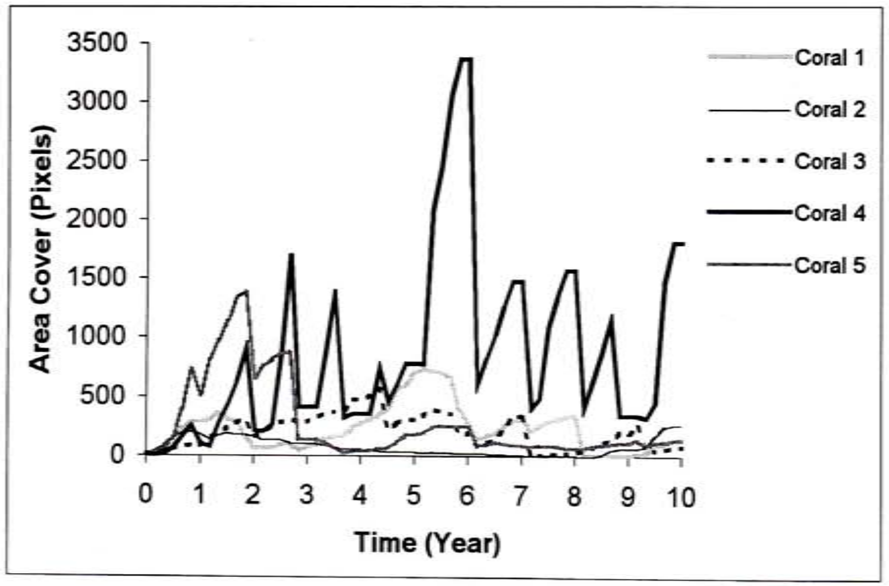


Figure A20. Change of area cover of each coral group in each simulation under fixed time high level of disturbance (50% area being disturbed each time).







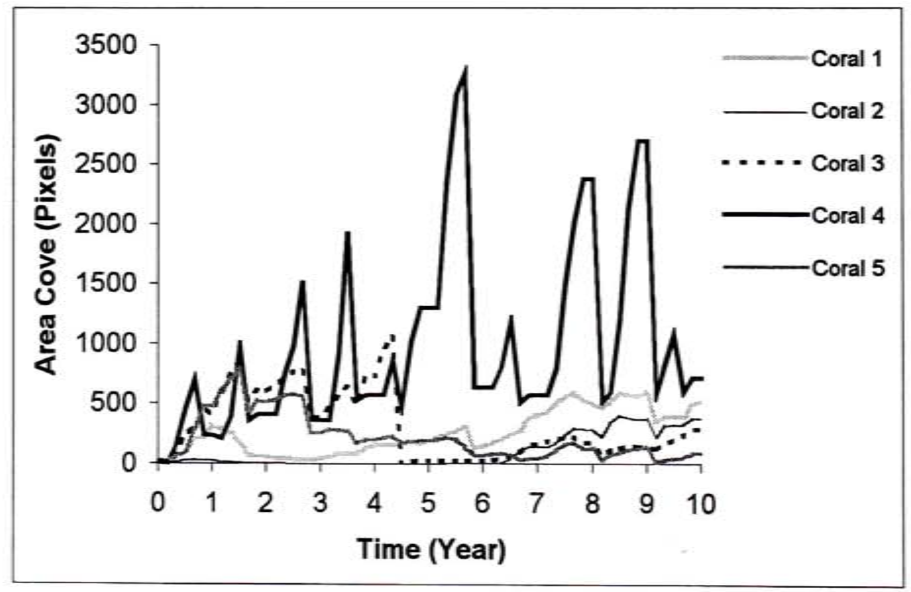


Figure A21. Change of area cover of each coral group in each simulation under random time intermediate level of disturbance (25% area being disturbed each time).

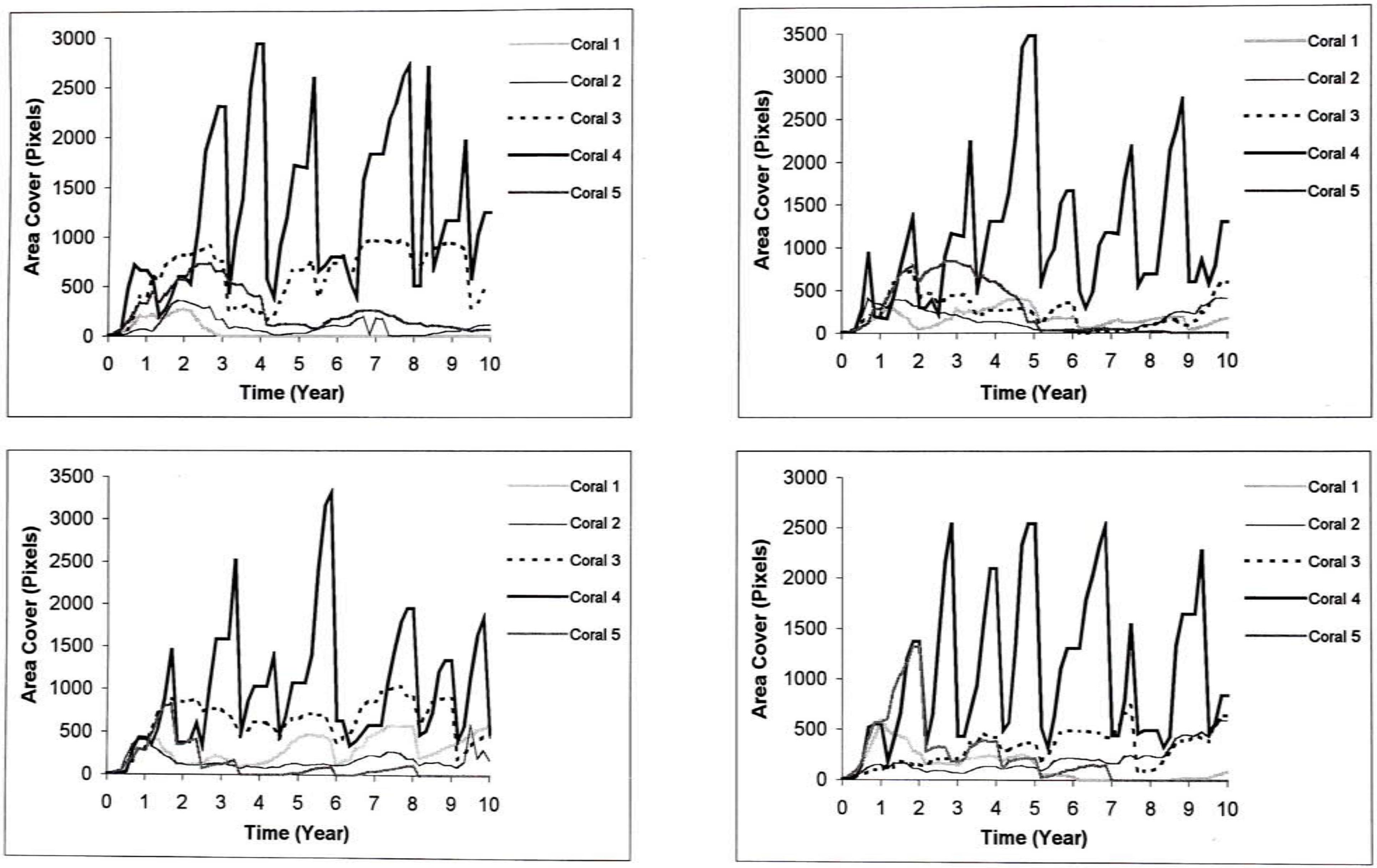


Figure A22. Change of area cover of each coral group in each simulation under random time intermediate level of disturbance (25% area being disturbed each time).

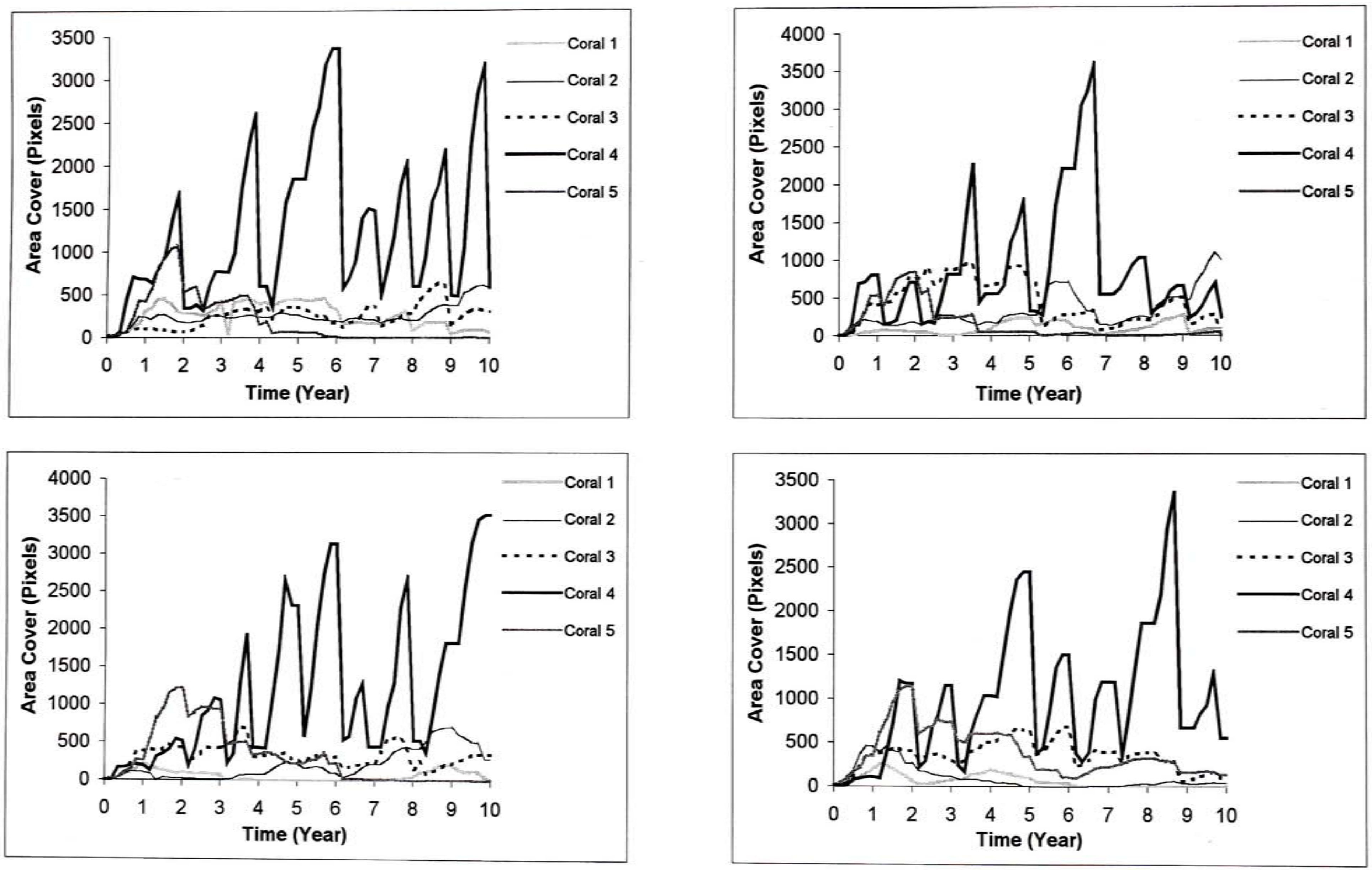


Figure A23. Change of area cover of each coral group in each simulation under random time intermediate level of disturbance (25% area being disturbed each time).

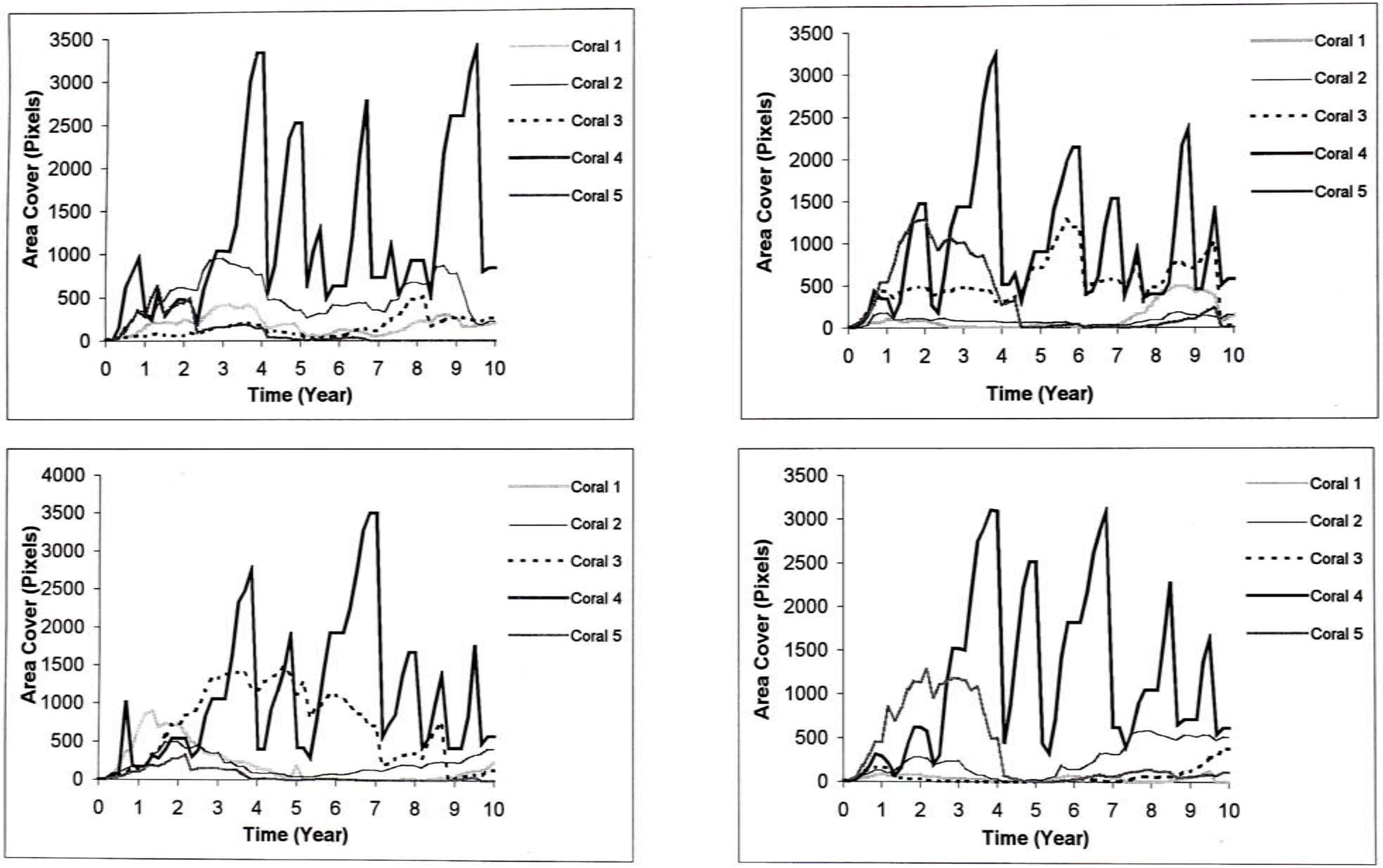


Figure A24. Change of area cover of each coral group in each simulation under random time intermediate level of disturbance (25% area being disturbed each time).

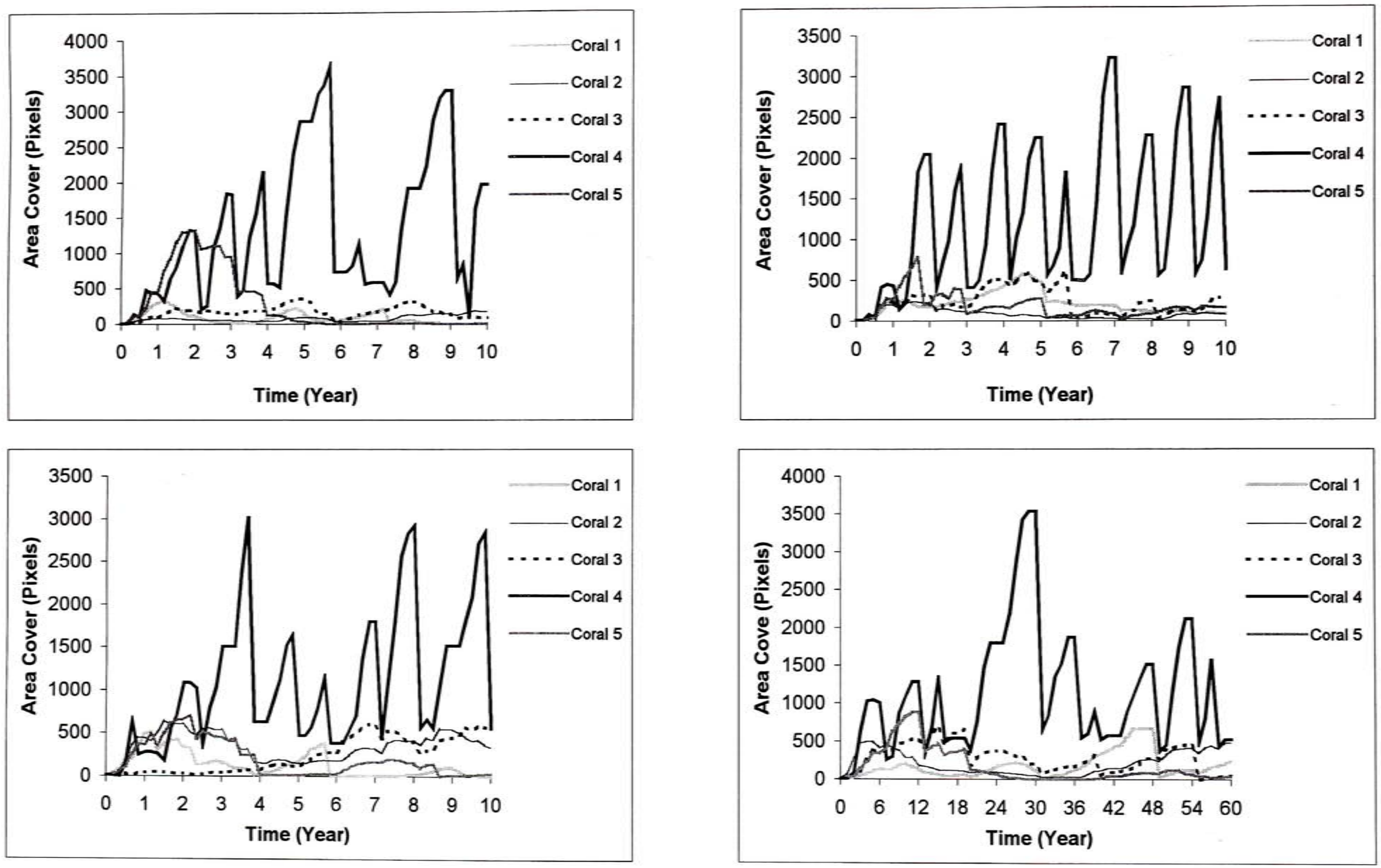


Figure A25. Change of area cover of each coral group in each simulation under random time intermediate level of disturbance (25% area being disturbed each time).